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OF THE

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PROCEEDINGS

OF THE

ROYAL SOCIETY OF EDINBURGH.

VOL. LVIII. 1937–38.

I.—Induction Proofs of the Relations between certain Asymptotic Expansions and Corresponding Generalised Hypergeometric Series. By **Professor T. M. MacRobert,** D.Sc.

(MS. received September 14, 1937. Read December 6, 1937.)

§ 1. *Introductory.*—The subject of this paper was studied by Orr (*Camb. Phil. Trans.*, vol. xvii, 1898, pp. 171–199; 1899, pp. 283–290), and later by Barnes (*Proc. Lond. Math. Soc.*, ser. 2, vol. v, 1906, pp. 59–116), in whose paper a number of references to earlier work on the subject are given. Formulæ equivalent to (9), (18), and (20) below were given by Barnes, who derived them by his well-known method of integrating products and quotients of Gamma Functions. In this paper the formulæ are deduced by induction from simpler formulæ which are established in section 2. In order to simplify the notation, four functions, denoted by P, E, Q, and H, are introduced, the first two in section 3, the last two in section 5. The P and Q functions are merely generalised hypergeometric functions multiplied by convenient factors. The E function, which is equivalent to Barnes's contour integral, is defined as a multiple integral, and from it the asymptotic expansion, with a useful form for the remainder, is easily derived. The H function is a multiple of the E function.

The relations between the P and E functions are established in sections 4 and 5, the asymptotic expansions in section 6, while in section 7 some integrals involving hypergeometric and Legendre Functions are evaluated in terms of E functions.

§ 2. *Preliminary Formulæ.*—Consider the integral

$$\mathrm{I} \equiv \int_{\mathrm{K}} e^{\zeta x} \zeta^{\beta-1} (\zeta - 1)^{-\alpha} d\zeta,$$

where x is real and positive, the contour K starts from and ends at $-\infty$ on the real axis, passing in the positive direction round the point $\zeta=1$, and amp ζ, amp $(\zeta-1)$ are both equal to $-\pi$ initially. Deform the contour in such a way that $|\zeta|>1$ at all points on it and expand $(\zeta-1)^{-a}$ in descending powers of ζ. Then, since

$$\int_K e^{\zeta}\zeta^{-z}d\zeta=\frac{2\pi i}{\Gamma(z)}, \qquad (1)$$

$$I=\frac{2\pi i x^{a-\beta}}{\Gamma(a-\beta+1)}\,{}_1F_1(a;\ a-\beta+1;\ x).$$

Again, deform the contour K into segments of the ξ-axis, with small semicircles at $\zeta=0$ and a small circle at $\zeta=1$. Then, if $R(\beta)>0$, $R(1-a)>0$, the integrals round these curves tend to zero with their radii, and we get

$$I=2i\sin a\pi\int_0^1 e^{x\xi}\xi^{\beta-1}(1-\xi)^{-a}d\xi$$
$$+2i\sin(\beta-a)\pi\int_0^\infty e^{-\lambda x}\lambda^{\beta-1}(1+\lambda)^{-a}d\lambda.$$

Now, if $R(\beta)>0$, $R(1-a)>0$,

$$\int_0^1 e^{x\xi}\xi^{\beta-1}(1-\xi)^{-a}d\xi=B(\beta,\ 1-a)\,{}_1F_1(\beta;\ \beta-a+1;\ x);. \qquad (2)$$

and therefore, if

$$P(a;\ \beta;\ x)\equiv\Gamma(\beta-a)\Gamma(a)x^{a}\,{}_1F_1(a;\ a-\beta+1;\ x), \qquad (3)$$

it follows that

$$P(a;\ \beta;\ x)+P(\beta;\ a;\ x)=\Gamma(a)x^{\beta}\int_0^\infty e^{-\lambda x}\lambda^{\beta-1}(1+\lambda)^{-a}d\lambda, \qquad (4)$$

where $R(\beta)>0$ and $|\text{amp}\,x|<\frac{1}{2}\pi$. The restriction $R(1-a)>0$ is removed by applying the method of Analytical Continuation.

The formula

$$P(a;\ \beta;\ x)=\frac{\sin\beta\pi}{\sin(\beta-a)\pi}\Gamma(\beta)x^{a}\int_0^1 e^{xt}t^{a-1}(1-t)^{-\beta}dt, \qquad (5)$$

where $R(a)>0$, $R(1-\beta)>0$, will also be required. It is derived from (3) and (2).

Again, if C is a contour passing from infinity positively round the origin to infinity, the initial and final directions making angles $-\pi+\phi$, $\pi-\phi$ with the real axis, where ϕ is a positive acute angle, and if x is real and positive and amp ζ, amp $(1+\zeta/x)$ both have the value $-\pi+\phi$ initially,

$$\int_C e^{\zeta}\zeta^{\beta-1}\left(1+\frac{\zeta}{x}\right)^{-a}d\zeta=x^{a}\int_C\frac{e^{\zeta}}{\zeta^{a-\beta+1}}\left(1+\frac{x}{\zeta}\right)^{-a}d\zeta=\frac{2\pi i x^{a}}{\Gamma(a-\beta+1)}\,{}_1F_1(a;\ a-\beta+1;\ -x),$$

as can be seen by expanding $(1+x/\zeta)^{-a}$ in descending powers of ζ and integrating term by term.

Now (4) may be written

$$P(\alpha;\ \beta;\ x)+P(\beta;\ \alpha;\ x)=\Gamma(\alpha)\int_0^\infty e^{-\lambda}\lambda^{\beta-1}\left(1+\frac{\lambda}{x}\right)^{-\alpha}d\lambda, \quad . \quad . \quad (4')$$

and in this form it is valid for $R(\beta)>0$, $|\operatorname{amp} x|<\pi$. Let the λ-axis be turned through a negative acute angle. Then (4′) is valid when $\operatorname{amp} x=-\pi$. Replace x by $xe^{-i\pi}$, where x is real and positive, and (4′) becomes

$$\begin{aligned}&\Gamma(\beta-\alpha)\Gamma(\alpha)(xe^{-i\pi})^{\alpha}{}_1F_1(\alpha;\ \alpha-\beta+1;\ xe^{-i\pi})\\&+\Gamma(\alpha-\beta)\Gamma(\beta)(xe^{-i\pi})^{\beta}{}_1F_1(\beta;\ \beta-\alpha+1;\ xe^{-i\pi})\\&\qquad=\Gamma(\alpha)\int_0^\infty e^{-\lambda}\lambda^{\beta-1}\left(1+\frac{\lambda}{xe^{-i\pi}}\right)^{-\alpha}d\lambda,\end{aligned}$$

where $R(\beta)>0$, x is real and positive, and λ makes a negative acute angle with the real axis.

Hence

$$\begin{aligned}&\frac{\Gamma(\alpha)e^{-i\alpha\pi}}{2i\sin(\beta-\alpha)\pi}\int_C e^{\zeta}\zeta^{\beta-1}\left(1+\frac{\zeta}{x}\right)^{-\alpha}d\zeta\\&+\frac{\Gamma(\beta)e^{-i\beta\pi}}{2i\sin(\alpha-\beta)\pi}\int_C e^{\zeta}\zeta^{\alpha-1}\left(1+\frac{\zeta}{x}\right)^{-\beta}d\zeta\\&\qquad=\Gamma(\alpha)\int_0^\infty e^{-\lambda}\lambda^{\beta-1}\left(1+\frac{\lambda}{xe^{-i\pi}}\right)^{-\alpha}d\lambda, \quad . \quad (6)\end{aligned}$$

where $R(\beta)>0$, x is real and positive, and λ makes a negative acute angle with the real axis.

§ 3. *Notation.*—Employing the usual notation for the generalised hypergeometric function, we write

$$\begin{aligned}P(\alpha_r;\ p-1,\ \alpha_s:q,\ \rho_t:x)&\equiv\frac{\prod\limits_{s=1}^{p}{}'\,\Gamma(\alpha_s-\alpha_r)}{\prod\limits_{t=1}^{q}\Gamma(\rho_t-\alpha_r)}\\&\times\Gamma(\alpha_r)x^{\alpha_r}{}_{q+1}F_{p-1}\left\{\begin{matrix}\alpha_r,\ \alpha_r-\rho_1+1,\ \alpha_r-\rho_2+1,\ \ldots,\ \alpha_r-\rho_q+1;\ (-1)^{p-q}x\\\alpha_r-\alpha_1+1,\ \alpha_r-\alpha_2+1,\ \ldots *\ldots,\ \alpha_r-\alpha_p+1\end{matrix}\right\}, \quad (7)\end{aligned}$$

the * denoting that the term $\alpha_r-\alpha_r+1$ is omitted. It is assumed that the constants are such that the functions exist.

Again, if $|\operatorname{amp} x|<\pi$,

$$\begin{aligned}E(p,\ \alpha_r:q,\ \rho_s:x)&\equiv\frac{\Gamma(\alpha_{q+1})}{\Gamma(\rho_1-\alpha_1)\Gamma(\rho_2-\alpha_2)\ \ldots\ \Gamma(\rho_q-\alpha_q)}\\&\times\prod_{\mu=1}^{q}\int_0^\infty\lambda_\mu^{\rho_\mu-\alpha_\mu-1}(1+\lambda_\mu)^{-\rho_\mu}d\lambda_\mu\prod_{\nu=2}^{p-q-1}\int_0^\infty e^{-\lambda_{q+\nu}}\lambda_{q+\nu}^{\alpha_{q+\nu}-1}d\lambda_{q+\nu}\\&\times\int_0^\infty e^{-\lambda_p}\lambda_p^{\alpha_p-1}\left\{1+\frac{\lambda_{q+2}\lambda_{q+3}\ \ldots\ \lambda_p}{(1+\lambda_1)(1+\lambda_2)\ \ldots\ (1+\lambda_q)x}\right\}^{-\alpha_{q+1}}d\lambda_p, \quad . \quad (8)\end{aligned}$$

the constants being such that the integrals are convergent.

Note.—It is sometimes convenient to write $\mathrm{E}\begin{pmatrix} \alpha_1, & \alpha_2, & \ldots, & \alpha_p : x \\ \rho_1, & \rho_2, & \ldots, & \rho_q \end{pmatrix}$ instead of $\mathrm{E}(p, \alpha_r : q, \rho_s : x)$. If there are no ρ's the function may be written $\mathrm{E}(p, \alpha_r : 0 : x)$ or $\mathrm{E}(\alpha_1, \alpha_2, \ldots, \alpha_p : 0 : x)$.

§ 4. *Expression for the E Function in Terms of P Functions.*—The formula to be proved is

$$\mathrm{E}(p, \alpha_r : q, \rho_s : x) = \sum_{r=1}^{p} \mathrm{P}(\alpha_r ; p-1, \alpha_s : q, \rho_t : x), \quad . \quad . \quad (9)$$

where $p \geqq q+2$.

CASE I: *q Zero.*—Here

$$\mathrm{P}(\alpha_r ; p-1, \alpha_s : 0 : x) = \prod_{s=1}^{p}{}' \Gamma(\alpha_s - \alpha_r)$$
$$\times \Gamma(\alpha_r) x^{\alpha_r} {}_1\mathrm{F}_{p-1}\{\alpha_r ;\ \alpha_r - \alpha_1 + 1, \ldots * \ldots, \alpha_r - \alpha_p + 1 ;\ (-1)^p x\}, \quad (10)$$

and it is required to prove that

$$\sum_{r=1}^{p} \mathrm{P}(\alpha_r ; p-1, \alpha_s : 0 : x) = \mathrm{E}(p, \alpha_r : 0 : x)$$
$$= \Gamma(\alpha_1) \prod_{\nu=2}^{p-1} \int_0^\infty e^{-\lambda_\nu} \lambda_\nu^{\alpha_\nu - 1} d\lambda_\nu \int_0^\infty e^{-\lambda_p} \lambda_p^{\alpha_p - 1} \left(1 + \frac{\lambda_2 \lambda_3 \ldots \lambda_p}{x}\right)^{-\alpha_1} d\lambda_p. \quad (11)$$

Assume that x is real and positive. Then, if (11) is valid,

$$\int_0 e^{\zeta} \zeta^{\alpha_{p+1}-1} \sum_{r=1}^{p} \mathrm{P}\left(\alpha_r ; p-1, \alpha_s : 0 : \frac{x}{\zeta}\right) d\zeta$$
$$= \sum_{r=1}^{p} 2i \sin(\alpha_{p+1} - \alpha_r)\pi\, e^{i\alpha_r \pi} \mathrm{P}(\alpha_r ; p, \alpha_s : 0 : xe^{-i\pi}) = \Gamma(\alpha_1) \prod_{\nu=2}^{p} \int_0^\infty e^{-\lambda_\nu} \lambda_\nu^{\alpha_\nu - 1} d\lambda_\nu$$
$$\times \int_0 e^{\zeta} \zeta^{\alpha_{p+1}-1} \left(1 + \frac{\lambda_2 \lambda_3 \ldots \lambda_p \zeta}{x}\right)^{-\alpha_1} d\zeta.$$

Next divide by $2i \sin(\alpha_{p+1} - \alpha_1)\pi e^{i\alpha_1 \pi}$, and then interchange α_1 and α_{p+1} and add the two equations. Thus, since

$$\sin(\alpha_{p+1} - \alpha_r)\pi\, e^{-i(\alpha_1 - \alpha_r)\pi} - \sin(\alpha_1 - \alpha_r)\pi\, e^{-i(\alpha_{p+1} - \alpha_r)\pi} = \sin(\alpha_{p+1} - \alpha_1)\pi,$$

we have, from formula (6), with λ_{p+1} for λ,

$$\sum_{r=1}^{p+1} \mathrm{P}(\alpha_r ; p, \alpha_s : 0 : xe^{-i\pi}) = \Gamma(\alpha_1) \prod_{\nu=2}^{p} \int_0^\infty e^{-\lambda_\nu} \lambda_\nu^{\alpha_\nu - 1} d\lambda_\nu$$
$$\times \int_0^\infty e^{-\lambda_{p+1}} \lambda_{p+1}^{\alpha_{p+1} - 1} \left(1 + \frac{\lambda_2 \lambda_3 \ldots \lambda_{p+1}}{xe^{-i\pi}}\right)^{-\alpha_1} d\lambda_{p+1}.$$

Now let amp x increase by π, at the same time making amp λ_{p+1} tend to zero, and write $xe^{i\pi}$ for x, so that x is then real and positive; thus

$$\sum_{r=1}^{p+1} \mathrm{P}(\alpha_r ; p, \alpha_s : 0 : x) = \mathrm{E}(p+1, \alpha_r : 0 : x).$$

It follows that, if (11) holds for the value p of p, it also holds for the value $p+1$. But from (4′) we see that it holds when $p=2$. Hence it holds for all positive integral values of p greater than unity.

CASE II: *q any Positive Integer.*—Assume that (9) is valid, and note that, if $R(\rho_{q+1}-\alpha_{p+1})>0$, $R(\alpha_r-\rho_{q+1}+1)>0$, $r=1, 2, \ldots, p$,

$$\int_0^1 t^{-\rho_{q+1}}(1-t)^{\rho_{q+1}-\alpha_{p+1}-1}P(\alpha_r;\ p-1,\ \alpha_s:q,\ \rho_t:xt)\,dt$$

$$=\frac{\sin(\alpha_{p+1}-\alpha_r)\pi}{\sin(\rho_{q+1}-\alpha_r)\pi}\Gamma(\rho_{q+1}-\alpha_{p+1})P(\alpha_r;\ p,\ \alpha_s:q+1,\ \rho_t:x),$$

where

$$r=1, 2, 3, \ldots, p.$$

Then if in $E(p,\ \alpha_r:q,\ \rho_s:xt)$ we put $\lambda_p(1+\lambda_1)(1+\lambda_2)\ldots(1+\lambda_q)xt$ for λ_p, we have

$$\sum_{r=1}^{p}\frac{\sin(\alpha_{p+1}-\alpha_r)\pi}{\sin(\rho_{q+1}-\alpha_r)\pi}\Gamma(\rho_{q+1}-\alpha_{p+1})P(\alpha_r;\ p,\ \alpha_s:q+1,\ \rho_t:x)$$

$$=\frac{\Gamma(\alpha_{q+1})x^{\alpha_p}}{\Gamma(\rho_1-\alpha_1)\Gamma(\rho_2-\alpha_2)\ldots\Gamma(\rho_q-\alpha_q)}\prod_{\mu=1}^{q}\int_0^\infty\lambda_\mu^{\rho_\mu-\alpha_\mu-1}(1+\lambda_\mu)^{\alpha_p-\rho_\mu}d\lambda_\mu$$

$$\times\prod_{\nu=q+2}^{p-1}\int_0^\infty e^{-\lambda_\nu}\lambda_\nu^{\alpha_\nu-1}d\lambda_\nu\int_0^\infty\lambda_p^{\alpha_p-1}(1+\lambda_{q+2}\lambda_{q+3}\ldots\lambda_p)^{-\alpha_{q+1}}d\lambda_p$$

$$\times\int_0^1 e^{-\lambda_p(1+\lambda_1)(1+\lambda_2)\ldots(1+\lambda_q)xt}t^{\alpha_p-\rho_{q+1}}(1-t)^{\rho_{q+1}-\alpha_{p+1}-1}dt.$$

Now replace t by $1-t$, and employ formula (5), with $\rho_{q+1}-\alpha_{p+1}$ for α and $\rho_{q+1}-\alpha_p$ for β. Thus

$$L.H.S.=\frac{\sin(\alpha_{p+1}-\alpha_p)\pi}{\sin(\rho_{q+1}-\alpha_p)\pi}\,\frac{\Gamma(\alpha_{q+1})x^{\alpha_p+\alpha_{p+1}-\rho_{q+1}}}{\Gamma(\rho_1-\alpha_1)\Gamma(\rho_2-\alpha_2)\ldots\Gamma(\rho_q-\alpha_q)\Gamma(\rho_{q+1}-\alpha_p)}$$

$$\times\prod_{\mu=1}^{q}\int_0^\infty\lambda_\mu^{\rho_\mu-\alpha_\mu-1}(1+\lambda_\mu)^{\alpha_p+\alpha_{p+1}-\rho_\mu-\rho_{q+1}}d\lambda_\mu\prod_{\nu=q+2}^{p-1}\int_0^\infty e^{-\lambda_\nu}\lambda_\nu^{\alpha_\nu-1}d\lambda_\nu$$

$$\times\int_0^\infty e^{-\lambda_p(1+\lambda_1)(1+\lambda_2)\ldots(1+\lambda_q)x}\lambda_p^{\alpha_p+\alpha_{p+1}-\rho_{q+1}-1}(1+\lambda_{q+2}\lambda_{q+3}\ldots\lambda_p)^{-\alpha_{q+1}}$$

$$\times P\{\rho_{q+1}-\alpha_{p+1};\ \rho_{q+1}-\alpha_p;\ \lambda_p(1+\lambda_1)(1+\lambda_2)\ldots(1+\lambda_q)x\}d\lambda_p.$$

Next multiply by

$$\frac{\sin(\rho_{q+1}-\alpha_p)\pi}{\sin(\alpha_{p+1}-\alpha_p)\pi}\cdot\frac{1}{\Gamma(\rho_{q+1}-\alpha_{p+1})},$$

interchange α_{p+1} and α_p, and add, noting that

$$\sin(\alpha_{p+1}-\alpha_r)\pi\sin(\rho_{q+1}-\alpha_p)\pi-\sin(\alpha_p-\alpha_r)\pi\sin(\rho_{q+1}-\alpha_{p+1})\pi$$
$$=\sin(\rho_{q+1}-\alpha_r)\pi\sin(\alpha_{p+1}-\alpha_p)\pi.$$

Then, from formula (4), with $\rho_{q+1}-\alpha_p$ for α, $\rho_{q+1}-\alpha_{p+1}$ for β, and λ_{q+1} for λ, we have

$$\sum_{r=1}^{p+1}\mathrm{P}(\alpha_r;\, p,\, \alpha_s : q+1,\, \rho_t : x)=\frac{\Gamma(\alpha_{q+1})x^{\alpha_p}}{\Gamma(\rho_1-\alpha_1)\Gamma(\rho_2-\alpha_2)\;.\;.\;.\;\Gamma(\rho_q-\alpha_q)\Gamma(\rho_{q+1}-\alpha_{p+1})}$$

$$\times\prod_{\mu=1}^{q}\int_0^\infty \lambda_\mu^{\rho_\mu-\alpha_\mu-1}(1+\lambda_\mu)^{\alpha_p-\rho_\mu}d\lambda_\mu \prod_{\nu=q+2}^{p-1}\int_0^\infty e^{-\lambda_\nu}\lambda_\nu^{\alpha_\nu-1}d\lambda_\nu$$

$$\times\int_0^\infty \lambda_p^{\alpha_p-1}(1+\lambda_{q+2}\lambda_{q+3}\;.\;.\;.\;\lambda_p)^{-\alpha_{q+1}}d\lambda_p$$

$$\times\int_0^\infty e^{-\lambda_p(1+\lambda_1)(1+\lambda_2)\;.\;.\;.\;(1+\lambda_{q+1})x}\lambda_{q+1}^{\rho_{q+1}-\alpha_{p+1}-1}(1+\lambda_{q+1})^{\alpha_p-\rho_{q+1}}d\lambda_{q+1}.$$

Now replace λ_p by $\dfrac{\lambda_p}{(1+\lambda_1)(1+\lambda_2)\;.\;.\;.\;(1+\lambda_{q+1})x}$, then replace λ_{q+2}, λ_{q+3}, . . ., λ_p by λ_{q+3}, λ_{q+4}, . . ., λ_{p+1}, respectively, and α_{q+1}, α_{q+2}, . . ., α_p, α_{p+1} by α_{q+2}, α_{q+3}, . . ., α_{p+1}, α_{q+1} respectively, and get

$$\sum_{r=1}^{p+1}\mathrm{P}(\alpha_r;\, p,\, \alpha_s : q+1,\, \rho_t : x)=\mathrm{E}(p+1,\, \alpha_r : q+1,\, \rho_s : x).$$

Thus, if the formula (9) holds for the values p of p and q of q, it holds also for the values $p+1$ of p and $q+1$ of q. But, by Case I, it holds when $q=0$, $p \geqq 2$. Hence it holds for all greater integral values of p and q such that $p \geqq q+2$.

From (9) it is clear that the α's in E may be interchanged without altering the value of the function. The same is true of the ρ's.

From (9) and (7) it is also evident that if a ρ and an α in E are equal, these can be omitted from E.

From the formula

$$\mathrm{K}_n(x)=\sqrt{\left(\frac{\pi}{2x}\right)}\frac{1}{\Gamma(n+\frac{1}{2})}e^{-x}\int_0^\infty e^{-\lambda}\lambda^{n-\frac{1}{2}}\left(1+\frac{\lambda}{2x}\right)^{n-\frac{1}{2}}d\lambda$$

for the Modified Bessel Function of the Second Kind and (8), we deduce that

$$\mathrm{K}_n(x)=\frac{\cos n\pi}{\sqrt{(2\pi x)}}e^{-x}\mathrm{E}(\tfrac{1}{2}+n,\, \tfrac{1}{2}-n : 0 : 2x)\quad.\qquad.\qquad.\quad(12)$$

§ 5. *Linear Relations between the P and E Functions.*—It is not possible to express one P function in terms of E functions. Other linear relations between the functions, given by (15) below, may, however, be deduced from formula (9).

In order to simplify the formulæ, two new functions, Q and H, are employed; these are defined as follows:—

$$Q(m : \alpha_r;\ p-1,\ \alpha_s : q,\ \rho_t : x)$$
$$\equiv \frac{\sin(\alpha_p-\alpha_r)\pi\,\sin(\alpha_{p-1}-\alpha_r)\pi\ .\ .\ .\ \sin(\alpha_{p-m+1}-\alpha_r)\pi}{\sin(\rho_1-\alpha_r)\pi\,\sin(\rho_2-\alpha_r)\pi\ .\ .\ .\ \sin(\rho_m-\alpha_r)\pi}$$
$$\times P(\alpha_r;\ p-1,\ \alpha_s : q,\ \rho_t : x), \quad . \quad (13)$$

where $m=0,\ 1,\ 2,\ .\ .\ .,\ q$ and $r=1,\ 2,\ .\ .\ .,\ p-m$;

$$H(m : p,\ \alpha_r-\rho_t+1 : q-1,\ \overset{*}{\rho_s}-\rho_t+1;\ 2-\rho_t : x)$$
$$\equiv \frac{\sin(\rho_t-\alpha_p)\pi\,\sin(\rho_t-\alpha_{p-1})\pi\ .\ .\ .\ \sin(\rho_t-\alpha_{p-m+1})\pi}{\sin(\rho_t-\rho_1)\pi\,\sin(\rho_t-\rho_2)\pi\ .\ .\ .\ *\ .\ .\ .\ \sin(\rho_t-\rho_m)\pi}$$
$$\times\frac{x^{\rho_t-1}}{\sin(\rho_t-1)\pi}E(p,\ \alpha_r-\rho_t+1 : q-1,\ \overset{*}{\rho_s}-\rho_t+1;\ 2-\rho_t : x), \quad (14)$$

where the $*$ denotes that the term $\rho_t-\rho_t+1$ is omitted, $2-\rho_t$ takes the place of $\rho_q-\rho_t+1$, and $m=1,\ 2,\ .\ .\ .,\ q,\ t=1,\ 2,\ 3,\ .\ .\ .,\ m$.

The formula to be proved is

$$\sum_{r=1}^{p-m} Q(m : \alpha_r;\ p-1,\ \alpha_s : q,\ \rho_t : x)$$
$$= \frac{\sin(\alpha_p\pi)\,\sin(\alpha_{p-1}\pi)\ .\ .\ .\ \sin(\alpha_{p-m+1}\pi)}{\sin(\rho_1\pi)\,\sin(\rho_2\pi)\ .\ .\ .\ \sin(\rho_m\pi)}$$
$$\times E(p,\ \alpha_r : q,\ \rho_s : x)$$
$$+\sum_{t=1}^{m} H(m : p,\ \alpha_r-\rho_t+1 : q-1,\ \overset{*}{\rho_s}-\rho_t+1;\ 2-\rho_t : x), \quad . \quad (15)$$

where $m=0,\ 1,\ 2,\ .\ .\ .,\ q$.

Let it be assumed that (15) holds for a particular value of m. Replace

α_r by $\alpha_r-\rho_{m+1}+1$, $\quad r=1,\ 2,\ .\ .\ .,\ p$,
ρ_s by $\rho_s-\rho_{m+1}+1$, $\quad s=1,\ 2,\ .\ .\ .\ *\ .\ .\ .,\ q$,

and

ρ_{m+1} by $2-\rho_{m+1}$,

and multiply by $x^{\rho_{m+1}-1}$. Then, noting that $P(\alpha_r;\ p-1,\ \alpha_s : q,\ \rho_t : x)$ becomes

$$\frac{\sin(\alpha_r\pi)}{\sin(\rho_{m+1}-\alpha_r)\pi}P(\alpha_r;\ p-1,\ \alpha_s : q,\ \rho_t : x),$$

we have

$$\sum_{r=1}^{p-m-1}\frac{\sin(\alpha_r\pi)}{\sin(\alpha_{p-m}-\alpha_r)\pi}Q(m+1 : \alpha_r;\ p-1,\ \alpha_s : q,\ \rho_t : x)$$
$$+\frac{\sin(\alpha_{p-m}\pi)}{\sin(\rho_{m+1}-\alpha_{p-m})\pi}Q(m : \alpha_{p-m};\ p-1,\ \alpha_s : q,\ \rho_t : x)$$
$$= -\frac{\sin(\rho_{m+1}\pi)}{\sin(\rho_{m+1}-\alpha_{p-m})\pi}H(m+1 : p,\ \alpha_r-\rho_{m+1}+1 : q-1,\ \overset{*}{\rho_s}-\rho_{m+1}+1;\ 2-\rho_{m+1} : x)$$
$$-\sum_{t=1}^{m}\frac{\sin(\rho_t\pi)}{\sin(\rho_t-\alpha_{p-m})\pi}H(m+1 : p,\ \alpha_r-\rho_t+1 : q-1,\ \overset{*}{\rho_s}-\rho_t+1;\ 2-\rho_t : x). \quad (16)$$

Now (15) may be written

$$\sum_{r=1}^{p-m-1} \frac{\sin(\rho_{m+1}-\alpha_r)\pi}{\sin(\alpha_{p-m}-\alpha_r)\pi} Q(m+1 : \alpha_r;\ p-1,\ \alpha_s : q,\ \rho_t : x)$$

$$+Q(m : \alpha_{p-m};\ p-1,\ \alpha_s : q,\ \rho_t : x)$$

$$=\frac{\sin(\alpha_p\pi)\sin(\alpha_{p-1}\pi)\ .\ .\ .\ \sin(\alpha_{p-m+1}\pi)}{\sin(\rho_1\pi)\sin(\rho_2\pi)\ .\ .\ .\ \sin(\rho_m\pi)} E(p,\ \alpha_r : q,\ \rho_s : x)$$

$$+\sum_{t=1}^{m} \frac{\sin(\rho_t-\rho_{m+1})\pi}{\sin(\rho_t-\alpha_{p-m})\pi} H(m+1 : p,\ \alpha_r-\rho_t+1 : q-1,\ \overset{*}{\rho}_s-\rho_t+1;\ 2-\rho_t : x). \quad (17)$$

On multiplying (17) by $\dfrac{\sin(\alpha_{p-m}\pi)}{\sin(\rho_{m+1}\pi)}$ and (16) by $\dfrac{\sin(\rho_{m+1}-\alpha_{p-m})\pi}{\sin(\rho_{m+1}\pi)}$ and subtracting, noting that

$$\sin(\rho_{m+1}-\alpha_r)\pi\sin(\alpha_{p-m}\pi)-\sin(\rho_{m+1}-\alpha_{p-m})\pi\sin(\alpha_r\pi)$$
$$=\sin(\rho_{m+1}\pi)\sin(\alpha_{p-m}-\alpha_r)\pi,$$

$$\sin(\rho_t-\rho_{m+1})\pi\sin(\alpha_{p-m}\pi)+\sin(\rho_{m+1}-\alpha_{p-m})\pi\sin(\rho_t\pi)$$
$$=\sin(\rho_{m+1}\pi)\sin(\rho_t-\alpha_{p-m})\pi,$$

we obtain formula (15) with $m+1$ in place of m. But, when m is zero, (15) is (9). Hence the formula (15) holds for $m=0, 1, 2, \ldots, q$.

§ 6. *Asymptotic Expansions.*—The asymptotic expansion of the function $E(p,\ \alpha_r : q,\ \rho_s : x)$ can be obtained from formula (8) by expanding the last factor in it by the binomial theorem in the form

$$(1+z)^{-\alpha_{q+1}}=\sum_{n=0}^{k-1} T_n+\rho_k,$$

where

$$z=\frac{\lambda_{q+2}\lambda_{q+3}\ .\ .\ .\ \lambda_p}{(1+\lambda_1)(1+\lambda_2)\ .\ .\ .\ (1+\lambda_q)x},$$

$$T_n=(-1)^n\frac{\Gamma(\alpha_{q+1}+n)}{n!\,\Gamma(\alpha_{q+1})}z^n,\ n=0,\ 1,\ 2\ .\ .\ .,\ k,$$

and

$$\rho_k=T_k\int_0^1 k(1-t)^{k-1}(1+zt)^{-\alpha_{q+1}-k}dt.$$

By taking k large enough, any restrictions on the values of the α's and the ρ's, apart from the restriction that none of them should be zero or a negative integer, can now be removed.

On evaluating the integrals corresponding to the first k terms of this series, it is found that

$$E(p,\ \alpha_r : q,\ \rho_s : x)=\text{the first } k \text{ terms of the series } \frac{\prod_{r=1}^{p}\Gamma(\alpha_r)}{\prod_{s=1}^{q}\Gamma(\rho_s)}\,{}_pF_q\left(\alpha_r;\ \rho_s;\ -\frac{1}{x}\right)+R_k, \quad (18)$$

where R_k is equal to the *R.H.S.* of formula (8), with ρ_k in place of the binomial expression in the last line. If k is taken so large that $R(\alpha_{q+1}+k) > 0$, it can be shown that, if $x \neq 0$, $|\operatorname{amp} x| < \pi$,

$$|R_k| < C\,|T_k|,$$

where C is positive and is constant with regard to $|x|$. Thus $|R_k|$ can be made as small as we please by sufficiently increasing $|x|$.

This can be proved by the method employed by the author to obtain the asymptotic expansion of the Confluent Hypergeometric Function (*Proc. Roy. Soc. Edin.*, vol. xlii, 1922, pp. 89, 90). The method is worked out in detail for the Modified Bessel Function $K_n(z)$ in the author's *Complex Variable*, second edition, pages 271–273. As the axes $\lambda_{q+2}, \lambda_{q+3}, \ldots, \lambda_p$ can be swung through any positive or negative acute angles the result holds, if $x \neq 0$, for

$$-\tfrac{1}{2}(p-q+1)\pi < \operatorname{amp} x < \tfrac{1}{2}(p-q+1)\pi.$$

It is not, as a rule, possible to express a generalised hypergeometric function in terms of E functions, and so obtain its asymptotic expansion. The only exception is when $p=q+2$ and $R(x) < 0$. This can be shown as follows:—

If $m=q=p-2$, (15) becomes

$$\Gamma(\alpha_2-\alpha_1)\frac{\Gamma(\alpha_1-\rho_1+1)\Gamma(\alpha_1-\rho_2+1)\ .\ .\ .\ \Gamma(\alpha_1-\rho_{p-2}+1)}{\Gamma(\alpha_1-\alpha_p+1)\Gamma(\alpha_1-\alpha_{p-1}+1)\ .\ .\ .\ \Gamma(\alpha_1-\alpha_3+1)}\Gamma(\alpha_1)x^{\alpha_1}$$

$$\times\,{}_{p-1}F_{p-1}\begin{pmatrix}\alpha_1,\ \alpha_1-\rho_1+1,\ \alpha_1-\rho_2+1,\ .\ .\ .,\ \alpha_1-\rho_{p-2}+1;\ x\\ \alpha_1-\alpha_2+1,\ \alpha_1-\alpha_3+1,\ .\ .\ .,\ \alpha_1-\alpha_p+1\end{pmatrix}$$

+ the same function with α_1 and α_2 interchanged

$$=\frac{\sin(\alpha_p\pi)\sin(\alpha_{p-1}\pi)\ .\ .\ .\ \sin(\alpha_3\pi)}{\sin(\rho_1\pi)\sin(\rho_2\pi)\ .\ .\ .\ \sin(\rho_{p-2}\pi)}E(p,\ \alpha_r : p-2,\ \rho_s : x)$$

$$+\sum_{t=1}^{p-2}\frac{\sin(\rho_t-\alpha_p)\pi\,\sin(\rho_t-\alpha_{p-1})\pi\ .\ .\ .\ \sin(\rho_t-\alpha_3)\pi}{\sin(\rho_t-\rho_1)\pi\,\sin(\rho_t-\rho_2)\pi\ .\ .\ .\ *\ .\ .\ .\ \sin(\rho_t-\rho_{p-2})\pi}$$

$$\times\frac{x^{\rho_t-1}}{\sin(\rho_t-1)\pi}E(p,\ \alpha_r-\rho_t+1 : p-3,\ \overset{*}{\rho_s}-\rho_t+1;\ 2-\rho_t : x).$$

Now replace $\rho_1, \rho_2, \ldots, \rho_{p-2}$ by $\alpha_1-\alpha_2+1$, $\alpha_1-\alpha_3+1, \ldots, \alpha_1-\alpha_{p-1}+1$, respectively, and $\alpha_2, \alpha_3, \ldots, \alpha_p$ by $\alpha_1-\rho_1+1$, $\alpha_1-\rho_2+1, \ldots, \alpha_1-\rho_{p-1}+1$, respectively, and write p for $p-1$: then

$$\Gamma(1-\rho_1)\frac{\Gamma(\alpha_1)\Gamma(\alpha_2)\ .\ .\ .\ \Gamma(\alpha_p)}{\Gamma(\rho_p)\Gamma(\rho_{p-1})\ .\ .\ .\ \Gamma(\rho_2)}x^{\alpha_1}\,{}_pF_p\begin{pmatrix}\alpha_1,\ \alpha_2,\ .\ .\ .,\ \alpha_p;\ x\\ \rho_1,\ \rho_2,\ .\ .\ .,\ \rho_p\end{pmatrix}$$

$$+\Gamma(\rho_1-1)\frac{\Gamma(\alpha_1-\rho_1+1)\Gamma(\alpha_2-\rho_1+1)\ .\ .\ .\ \Gamma(\alpha_p-\rho_1+1)}{\Gamma(\rho_p-\rho_1+1)\Gamma(\rho_{p-1}-\rho_1+1)\ .\ .\ .\ \Gamma(\rho_2-\rho_1+1)}$$

$$\times\,x^{\alpha_1-\rho_1+1}\,{}_pF_p\begin{pmatrix}\alpha_1-\rho+{}_1 1,\ \alpha_2-\rho_1+1,\ .\ .\ .,\ \alpha_p-\rho_1+1;\ x\\ \rho_2-\rho_1+1,\ \rho_3-\rho_1+1,\ .\ .\ .,\ \rho_p-\rho_1+1,\ 2-\rho_1\end{pmatrix}$$

$$= \frac{\sin(\alpha_1-\rho_p+1)\pi \sin(\alpha_1-\rho_{p-1}+1)\pi \,.\,.\,.\, \sin(\alpha_1-\rho_2+1)\pi}{\sin(\alpha_1-\alpha_2+1)\pi \sin(\alpha_1-\alpha_3+1)\pi \,.\,.\,.\, \sin(\alpha_1-\alpha_p+1)\pi}$$

$$\times \mathrm{E}\left(\begin{matrix}\alpha_1, \alpha_1-\rho_1+1, \alpha_1-\rho_2+1, \,.\,.\,., \alpha_1-\rho_p+1 : x\\ \alpha_1-\alpha_2+1, \alpha_1-\alpha_3+1, \,.\,.\,., \alpha_1-\alpha_p+1\end{matrix}\right)$$

$$+ \sum_{s=2}^{p} \frac{\sin(\rho_p-\alpha_s)\pi \sin(\rho_{p-1}-\alpha_s)\pi \,.\,.\,.\, \sin(\rho_2-\alpha_s)\pi}{\sin(\alpha_2-\alpha_s)\pi \sin(\alpha_3-\alpha_s)\pi \,.\,.\,.\, * \,.\,.\,.\, \sin(\alpha_p-\alpha_s)\pi}$$

$$\times \frac{x^{\alpha_1-\alpha_s}}{\sin(\alpha_1-\alpha_s)\pi} \mathrm{E}\left(\begin{matrix}\alpha_s, \alpha_s-\rho_1+1, \alpha_s-\rho_2+1, \,.\,.\,., \alpha_s-\rho_p+1 : x\\ \alpha_s-\alpha_1+1, \alpha_s-\alpha_2+1, \,.\,.\,. * \,.\,.\,., \alpha_s-\alpha_p+1\end{matrix}\right). \quad (19)$$

It follows that, if $-\frac{1}{2}\pi < \operatorname{amp} x < \frac{1}{2}\pi$,

$$(xe^{\pm i\pi})^{\rho_1-1}\Gamma(\rho_1)\Gamma(1-\rho_1)\prod_{r=1}^{p}\frac{\Gamma(\alpha_r)}{\Gamma(\rho_r)}\, {}_pF_p\left(\begin{matrix}\alpha_1, \alpha_2, \,.\,.\,., \alpha_p;\ xe^{\pm i\pi}\\ \rho_1, \rho_2, \,.\,.\,., \rho_p\end{matrix}\right)$$

+ the second term on the *L.H.S.* divided by $x^{\alpha_1-\rho_1+1}$ and with $xe^{\pm i\pi}$ for x

$$= \sum_{s=1}^{p} (xe^{\pm i\pi})^{\rho_1-\alpha_s-1} \frac{\sin(\rho_2-\alpha_s)\pi \sin(\rho_3-\alpha_s)\pi \,.\,.\,.\, \sin(\rho_p-\alpha_s)\pi}{\sin(\alpha_1-\alpha_s)\pi \sin(\alpha_2-\alpha_s)\pi \,.\,.\,.\, * \,.\,.\,.\, \sin(\alpha_p-\alpha_s)\pi}$$

$$\times \mathrm{E}\left(\begin{matrix}\alpha_s, \alpha_s-\rho_1+1, \alpha_s-\rho_2+1, \,.\,.\,., \alpha_s-\rho_p+1 : xe^{\pm i\pi}\\ \alpha_s-\alpha_1+1, \alpha_s-\alpha_2+1, \,.\,.\,. * \,.\,.\,., \alpha_s-\alpha_p+1\end{matrix}\right).$$

On subtracting this formula with $e^{-i\pi}$ from the same formula with $e^{i\pi}$ we obtain an expression for the function ${}_pF_p$ in terms of $2p$ E's. On expanding the E's asymptotically the asymptotic expansion

$$\prod_{r=1}^{p}\frac{\Gamma(\alpha_r)}{\Gamma(\rho_r)}\, {}_pF_p\left(\begin{matrix}\alpha_1, \alpha_2, \,.\,.\,., \alpha_p;\ -x\\ \rho_1, \rho_2, \,.\,.\,., \rho_p\end{matrix}\right)$$

$$= \sum_{s=1}^{p} x^{-\alpha_s} \frac{\Gamma(\alpha_s)\Gamma(\alpha_1-\alpha_s)\Gamma(\alpha_2-\alpha_s) \,.\,.\,.\, * \,.\,.\,.\, \Gamma(\alpha_p-\alpha_s)}{\Gamma(\rho_1-\alpha_s)\Gamma(\rho_2-\alpha_s) \,.\,.\,.\, \Gamma(\rho_p-\alpha_s)}$$

$$\times {}_{p+1}F_{p-1}\left(\begin{matrix}\alpha_s, \alpha_s-\rho_1+1, \alpha_s-\rho_2+1, \,.\,.\,., \alpha_s-\rho_p+1;\ \frac{1}{x}\\ \alpha_s-\alpha_1+1, \alpha_s-\alpha_2+1, \,.\,.\,. * \,.\,.\,., \alpha_s-\alpha_p+1\end{matrix}\right), \quad . \quad (20)$$

where $|\operatorname{amp} x| < \frac{1}{2}\pi$, is obtained.

§ 7. *Integrals of Hypergeometric and Legendre Functions.*—Certain integrals will now be evaluated in terms of E functions; from these results expressions for the integrals in terms of generalised hypergeometric functions can then be deduced by means of (9).

For example, if $R(x) > 0$, $R(\gamma) > 0$,

$$\int_0^\infty e^{-x\lambda}\lambda^{\gamma-1}F(\alpha, \beta;\ \delta;\ -\lambda)d\lambda$$

$$= \int_0^\infty e^{-x\lambda}\lambda^{\gamma-1}d\lambda \frac{1}{B(\beta, \delta-\beta)}\int_0^\infty \mu^{\delta-\beta-1}(1+\mu)^{-\delta}\left(1+\frac{\lambda}{1+\mu}\right)^{-\alpha} d\mu$$

$$=\frac{\Gamma(\delta)x^{-\gamma}}{\Gamma(\beta)\Gamma(\delta-\beta)}\int_0^\infty \mu^{\delta-\beta-1}(1+\mu)^{-\delta}d\mu\int_0^\infty e^{-\lambda}\lambda^{\gamma-1}\left\{1+\frac{\lambda}{(1+\mu)x}\right\}^{-\alpha}d\lambda$$

$$=\frac{\Gamma(\delta)x^{-\gamma}}{\Gamma(\alpha)\Gamma(\beta)}E\begin{pmatrix}\alpha,\ \beta,\ \gamma : x\\ \delta\end{pmatrix} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (21)$$

$$=\frac{\Gamma(\delta)x^{-\gamma}}{\Gamma(\alpha)\Gamma(\beta)}\times\sum_{\alpha,\beta,\gamma}\frac{\Gamma(\beta-\alpha)\Gamma(\gamma-\alpha)}{\Gamma(\delta-\alpha)}\Gamma(\alpha)x^{\alpha}\,{}_2F_2\begin{pmatrix}\alpha,\ \alpha-\delta+1;\ x\\ \alpha-\beta+1,\ \alpha-\gamma+1\end{pmatrix}. \quad (22)$$

Again, consider the integral

$$\int e^{ix\zeta}F(\alpha,\ \beta;\ \gamma;\ \zeta)d\zeta,$$

where x is real and positive and $R(\gamma-\alpha-\beta) > -1$, taken round the contour bounded by the lines $\xi=0$, $\xi=1$, $\eta=0$, $\eta=k>0$, indented at $\zeta=0$ and $\zeta=1$. When k tends to infinity this gives

$$\int_0^1 e^{ix\xi}F(\alpha,\ \beta;\ \gamma;\ \xi)d\xi$$

$$-\int_0^\infty e^{-x\eta}F(\alpha,\ \beta;\ \gamma;\ i\eta)id\eta$$

$$+e^{ix}\int_0^\infty e^{-x\eta}\left[\begin{array}{l}\dfrac{\Gamma(\gamma-\alpha-\beta)\Gamma(\gamma)}{\Gamma(\gamma-\alpha)\Gamma(\gamma-\beta)}F(\alpha,\ \beta;\ \alpha+\beta-\gamma+1,\ -i\eta)\\ +\dfrac{\Gamma(\alpha+\beta-\gamma)\Gamma(\gamma)}{\Gamma(\alpha)\Gamma(\beta)}e^{-\frac{1}{2}i(\gamma-\alpha-\beta)\pi}\\ \times\eta^{\gamma-\alpha-\beta}F(\gamma-\alpha,\ \gamma-\beta;\ \gamma-\alpha-\beta+1;\ -i\eta)\end{array}\right]id\eta.$$

$$=0.$$

Hence, from (21),

$$\int_0^1 e^{ix\xi}F(\alpha,\ \beta;\ \gamma;\ \xi)d\xi$$

$$=\frac{ix^{-1}\Gamma(\gamma)}{\Gamma(\alpha)\Gamma(\beta)}E\begin{pmatrix}\alpha,\ \beta,\ 1 : ix\\ \gamma\end{pmatrix}$$

$$-\frac{ie^{ix}x^{-1}\Gamma(\gamma-\alpha-\beta)\Gamma(\alpha+\beta-\gamma+1)\Gamma(\gamma)}{\Gamma(\alpha)\Gamma(\beta)\Gamma(\gamma-\alpha)\Gamma(\gamma-\beta)}$$

$$\times\left\{\begin{array}{l}E\begin{pmatrix}\alpha, & \beta, & 1 & : & \dfrac{x}{i}\\ \alpha+\beta-\gamma+1\end{pmatrix}\\ -(ix)^{\alpha+\beta-\gamma}E\left(\gamma-\alpha,\ \gamma-\beta : 0 : \dfrac{x}{i}\right)\end{array}\right\}, \quad . \quad . \quad (23)$$

where, $-\pi < \text{amp}\ x < \pi$, $R(\gamma-\alpha-\beta) > -1$.

Again, on integrating,

$$e^{ix\zeta}(1-\zeta^2)^{\frac{1}{2}m}T_n^{-m}(\zeta),$$

where x is real and positive and $R(m) > -1$ round the contour bounded by $\xi = -1$, $\xi = +1$, $\eta = 0$, $\eta = k > 0$, indented at -1 and $+1$, and making k tend to infinity, we get

$$
\begin{aligned}
&\int_{-1}^{1} e^{ix\xi}(1-\xi^2)^{\frac{1}{2}m}\mathrm{T}_n^{-m}(\xi)\,d\xi \\
&\quad = -e^{ix-m\pi i}\frac{2^{m+1}}{\Gamma(m+1)}\int_0^\infty e^{-2x\eta}(i\eta)^m\mathrm{F}(-n,\ n+1;\ m+1;\ -i\eta)\,i\,d\eta \\
&\qquad + e^{-ix}\int_0^\infty e^{-2x\eta}\left[\begin{aligned}&\frac{\Gamma(m)2^{m+1}}{\Gamma(m+n+1)\Gamma(m-n)}\mathrm{F}(1-m+n,\ -m-n;\ 1-m;\ i\eta)\\ &+\frac{\Gamma(-m)2^{m+1}}{\Gamma(n+1)\Gamma(-n)}(i\eta)^m\mathrm{F}(-n,\ n+1;\ m+1;\ i\eta)\end{aligned}\right]i\,d\eta \\
&\quad = \frac{e^{ix}(ix)^{-m-1}}{\Gamma(-n)\Gamma(n+1)}\mathrm{E}\left(-n,\ n+1:0:\frac{2x}{i}\right) \\
&\qquad - \frac{e^{-ix}(ix)^{-1}2^m\Gamma(m)\Gamma(1-m)}{\Gamma(m+n+1)\Gamma(m-n)\Gamma(1-m+n)\Gamma(-m-n)}\mathrm{E}\left(\begin{matrix}1-m+n,\ -m-n,\ 1 : 2ix\\ 1-m\end{matrix}\right) \\
&\qquad + \frac{e^{-ix}(i/x)^{m+1}\Gamma(-m)\Gamma(m+1)}{\Gamma(n+1)\Gamma(-n)\Gamma(n+1)\Gamma(-n)}\mathrm{E}(-n,\ n+1:0:2ix),
\end{aligned}
$$

where $-\pi < \operatorname{amp} x < \pi$, $\mathrm{R}(m) > -1$.

Hence, from (21),

$$
\begin{aligned}
&\int_{-1}^{1} e^{x\xi}(1-\xi^2)^{\frac{1}{2}m}\mathrm{T}_n^{-m}(\xi)\,d\xi \\
&\quad = \sqrt{\left(\frac{2}{\pi}xe^{-i\pi}\right)}x^{-m-1}\mathrm{K}_{n+\frac{1}{2}}(xe^{-i\pi}) \\
&\qquad + \sqrt{\left(\frac{2}{\pi}x\right)}(xe^{-i\pi})^{-m-1}\frac{\sin n\pi}{\sin m\pi}\mathrm{K}_{n+\frac{1}{2}}(x) \\
&\qquad + \frac{\sin(m-n)\pi\sin(m+n)\pi}{\sin(m\pi)2^{-m}\pi}\frac{e^{-x}}{x}\mathrm{E}\left(\begin{matrix}1-m+n,\ -m-n,\ 1 : 2x\\ 1-m\end{matrix}\right), \quad . \qquad (24)
\end{aligned}
$$

where $-\frac{1}{2}\pi < \operatorname{amp} x < \frac{3}{2}\pi$, $\mathrm{R}(m) > -1$.

Next, if $\mathrm{R}(x) > 0$, $\mathrm{R}(m+1) > 0$,

$$
\begin{aligned}
&\int_{1}^{\infty} e^{-x\lambda}(\lambda^2-1)^{\frac{1}{2}m}\mathrm{Q}_n^{-m}(\lambda)\,d\lambda \\
&\quad = -\frac{\pi}{2\sin m\pi}\int_1^\infty e^{-x\lambda}\left\{\begin{aligned}&\frac{1}{\Gamma(1+m)}(\lambda-1)^m\mathrm{F}\left(-n,\ n+1;\ 1+m;\ \frac{1-\lambda}{2}\right)\\ &-\frac{\Gamma(n-m+1)}{\Gamma(n+m+1)}\frac{2^m}{\Gamma(1-m)}\mathrm{F}\left(n-m+1,\ -n-m;\ 1-m;\ \frac{1-\lambda}{2}\right)\end{aligned}\right\}d\lambda \\
&\quad = -\frac{\pi 2^m}{\sin m\pi}e^{-x}\int_0^\infty e^{-2x\eta}\left\{\begin{aligned}&\frac{1}{\Gamma(1+m)}\eta^m\mathrm{F}(-n,\ n+1;\ 1+m;\ -\eta)\\ &-\frac{\Gamma(n-m+1)}{\Gamma(n+m+1)}\frac{1}{\Gamma(1-m)}\mathrm{F}(n-m+1,\ -n-m;\ 1-m;\ -\eta)\end{aligned}\right\}d\eta
\end{aligned}
$$

$$= -\frac{\pi 2^m}{\sin m\pi}e^{-x}\left[\frac{(2x)^{-m-1}}{\Gamma(-n)\Gamma(n+1)}E(-n, n+1 : 0 : 2x) - \frac{1}{\Gamma(n+m+1)}\frac{(2x)^{-1}}{\Gamma(-n-m)}E\left(\begin{matrix} n-m+1, & -n-m, & 1 : 2x \\ & 1-m & \end{matrix}\right)\right]$$

$$= -\sqrt{\left(\frac{\pi x}{2}\right)}\frac{x^{-m-1}}{\sin m\pi}K_{n+\frac{1}{2}}(x) - \frac{\sin (m+n)\pi}{\sin (m\pi)2^{-m+1}}\frac{e^{-x}}{x}E\left(\begin{matrix} n-m+1, & -n-m, & 1 : 2x \\ & 1-m & \end{matrix}\right). \qquad (25)$$

On eliminating the E function from (24) and (25) we get

$$\int_{-1}^{1} e^{x\xi}(1-\xi^2)^{\frac{1}{2}m}T_n^{-m}(\xi)d\xi + \frac{2}{\pi}\sin (m-n)\pi\int_{1}^{\infty} e^{-x\lambda}(\lambda^2-1)^{\frac{1}{2}m}Q_n^{-m}(\lambda)d\lambda$$

$$= \sqrt{\left(\frac{2}{\pi}xe^{-i\pi}\right)}x^{-m-1}\{K_{n+\frac{1}{2}}(xe^{-i\pi}) - e^{i(n+\frac{1}{2})\pi}K_{n+\frac{1}{2}}(x)\}$$

$$= \sqrt{(2\pi x)}x^{-m-1}I_{n+\frac{1}{2}}(x), \qquad (26)$$

where $R(x) > 0$, $R(m) > -1$. This formula was given by Macdonald (*Proc. Lond. Math. Soc.*, vol. xxxv, 1902, p. 430).

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II.—Quantitative Evolution. IV. Deductions from the BAT Curve.

By **Professor J. Small,** D.Sc., Department of Botany, Queen's University, Belfast. (With Two Figures.)

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THE preceding papers of this series have demonstrated (1) that there is a progressive increase of average Dp-age in the subdivisions of Compositæ which can be correlated with geological age as determined from other data (Small and Johnston, 1937); (2) that these Dp-ages, when placed on a time-scale of years, follow a peculiar exponential curve, called the BAT curve (Small, 1937, Q.E. II); (3) that the measure of age in years which is given by the BAT curve can be used successfully for the Grasses (Small, 1937, Q.E. III).

The curvilinear relation of Dp-age to time in years indicates clearly that some factor or factors have been omitted from Yule's formulæ (Yule, 1924). This curvature is regular, so that Yule's formulæ are definitely proved to be correct up to a point, while they are as definitely proved to be incomplete, for Compositæ and Grasses, rather than completely wrong. Yule himself (1924) noted facts which suggested "that great caution will have to be used in interpreting doubling-periods in terms of geological time." Dp-age is an index rather than a measure of actual age. Considering the substantial proportion of genera at zero time required to fit the data (Small and Johnston, 1937, pp. 35–36), Yule writes: "Such a result would presumably be shown in any case where the origin of the group was polyphyletic, but I think it may have another significance and one which will render the interpretation of the figures a matter of difficulty. . . . Consider the effect on a distribution of the advent of a 'cataclysm,' *e.g.* of a glacial epoch, killing off a large number of species" (Yule, 1924, p. 59).

Yule proceeds (*op. cit.*, pp. 78–84) to consider "continuous killing-out" and also "cataclysmic killing," so that he was undoubtedly prepared for species disappearing during the history of a group. Since there were then no data available for the correlation of Dp-ages with geological time, Yule was unable to decide which of his two methods, if either, gave a true explanation of what has happened in the past. We now have the advantage of the demonstrated correlation of Dp-age and time along the BAT curve and can from this obtain some idea of the past history of species and genera.

If a disintegration curve for uranium be plotted with the time-scale vertical, and the actual, not proportional, increase of weight from present to past horizontal, such a curve is exactly the same in general form as the BAT curve, which has time horizontal and Dp-ages vertical. There is no clear analogy indicated as yet, but this curious similarity certainly suggests that we may be dealing in Dp-age with a relation which, on the whole, has a determinate half life-period like uranium.

YEAR VALUE OF THE DP-AGE UNIT.

Taking the mid-points of the geological periods concerned as 6, 18, 32, 49, and 70 m.y., we get corresponding average tribal Dp-ages as 2·66, 4·19, 5·06, 5·46, 5·96 (Small, 1937, Q.E. II). Dividing the mid-point values by the respective Dp-ages we obtain apparent year values for the Dp-age unit as 6/2·66 or 2·256 m.y. for Pliocene; 18/4·19 or 4·296 m.y. for Miocene; 32/5·06 or 6·324 m.y. for Oligocene; 49/5·46 or 8·974 m.y. for Eocene; and 70/5·96 or 11·790 m.y. for Late Cretaceous. These apparent year values increase with time and are placed near a perfectly straight line in fig. 1. The increase in value closely approximates

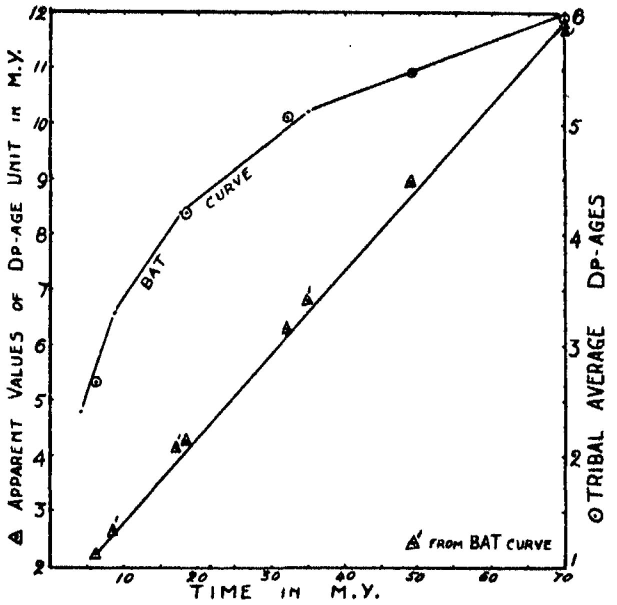

FIG. 1.—Apparent year values of the Dp-age unit.

a rectilinear relation; the increase calculated per one million years being 0·170 m.y. Pliocene to Miocene; 0·145 m.y. Miocene to Oligocene; 0·156 m.y. Oligocene to Eocene; 0·134 m.y. Eocene to Late Cretaceous, giving a mean increase of 0·152±0·018 m.y. per one million years.

This increase in the apparent year value of the Dp-age can similarly be calculated from the BAT curve, giving four points (fig. 1) which again closely approach the straight line, showing a mean increase above the second point of 0·155±0·018 m.y. per one million years. It is thus demonstrated that this increase, in the apparent length of the Dp-age unit, is directly proportional to time (fig. 1). Therefore, there seems to be no reason to suppose that the average apparent increase in the Dp-age unit is affected significantly by any other factor than time, to which it is directly proportional within narrow limits.

THE "K" FACTOR.

Since there is no reason to suppose that there has been an actual regular decrease in the length of the doubling period (Dp-age unit) with the progress of time, we are led to the conclusion that the apparent decrease (past to present) is due to the effect of some factor which acts upon the Dp-age, as calculated, in such a way that it decreases the value of the

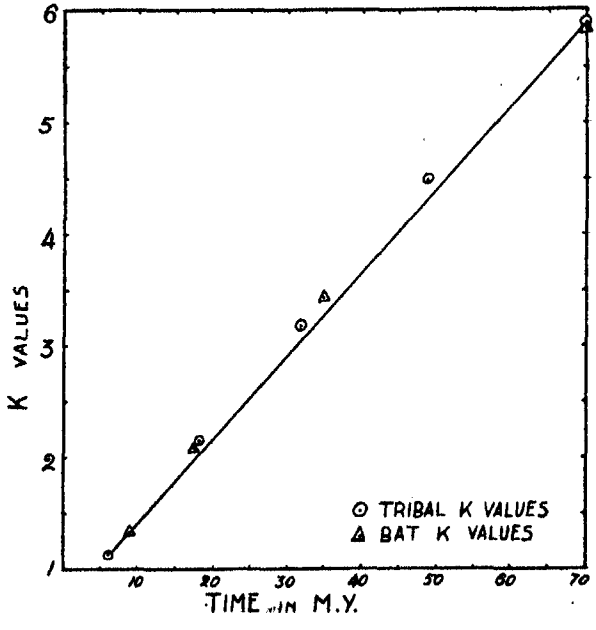

FIG. 2.—The relation of K values to time.

calculated Dp-age directly in proportion to the actual age of the group of genera. The effect (K) of this factor increases directly with time, along a straight line similar to that in fig. 1. The fact that K does increase directly with time can be shown graphically (fig. 2) or by calculating the degree to which Dp-age is decreased by K. Taking the top end, if the Dp-age unit is really about 2 m.y. (Small, 1937, Q.E. II), then at 70 m.y. we should get a Dp-age of 35 instead of the 5·96 or 6·0 which is observed; therefore 35/6 or 5·83 is the measure of K at 70 m.y. The free Dp-ages are 6/2 or 3, 18/2 or 9, 32/2 or 16, 49/2 or 24·5, and 70/2 or 35. These divided by the observed Dp-ages are 3/2·66 or *1·128*; 9/4·19 or *2·148*; 16/5·06 or *3·162*; 24·5/5·46 or *4·487* m. and 35/5·96 or *5·872*. The values in italics are the numerical values of K which increase along a straight line (fig. 2), with a mean increase of ·0755 ± ·0095 per 1 m.y. The K values calculated from the BAT curve are very similar (fig. 2) and show a mean increase of ·0780 ± ·0085 per 1 m.y.

The rectilinear relation of K and time being established, we must consider the logical consequences.

THE NORMAL DEATH OF SPECIES AND GENERA.

The only source of the depressing factor which gives the K values is the disappearance of species (and genera) with time. If species of Compositæ did double in number every two million years and all had survived up to the present time, there should be 2^{35} or over 34,363 millions of species instead of only about 10,000. Clearly species have disappeared on a large scale; the calculations are here in agreement with the fossil record. There is here no serious suggestion that there ever have been as many species in existence, even taking the whole of the geological history of Compositæ, but the number given shows conclusively that the total species-number has not doubled every 2 m.y. Breaks in the increase have occurred just as they do in the letter circles which are from time to time started in the hope of building a hospital with old stamps.

This disappearance of species (and genera) is a well-known phenomenon in the geological record, but up to the present species have been considered as having disappeared under the action of cataclysms or other external destructive factors. The factor giving K values yields measurable effects, and, when measured, these effects as K values are shown to be directly proportional to time. The hypothetical cataclysms must, therefore, have been distributed in time with a regularity greater than any geological cataclysmic hypothesis should be called upon to endure. The very nature of the geological cataclysm includes an irregularity of occurrence which is clearly not in accordance with the regular action of the K factor, as here demonstrated for Compositæ and as applying also to the Grasses (Small, 1937, Q.E. III). Thus we are compelled to consider factors which might act with regularity throughout time.

Since the dying-out, as measured by the K values, is directly proportional to time, it would appear that time itself could operate upon the life of species. Time as a regular factor can operate only through age of species and genera, and if species die out because of age the ultimate cause of death can only be old age or senescent sterility. So long as individuals of the species continue to produce viable seeds the species will survive, so that a natural or normal death of the species can occur only through increasing sterility of all individuals. This sterility would be one result of senescence in the species as a whole. Another result might be a restriction of the range of conditions within which the species can survive, leading to special local habitats where the species would be more liable to extinction by a local cataclysm.

The normal death of species of Angiosperms is in accordance with all known facts, and accounts, in part at least, for the rectilinear increase of K with time, as well as for many facts of species-number in various groups of plants other than Compositæ. It has already been shown to be in accordance with species-number in the Grasses (Small, 1937, Q.E. III, fig. 1); but the data for Birds indicate an average of 50 per cent. for elimination by competition.

Local cataclysms might kill all the individuals of local species, but could not affect the existence of the larger numbers of more widespread species; while the general cataclysms required to fit the data are too numerous for the geological record. Yule uses up to 100 cataclysms in 100 million years, and obtains a value of 2·1 m.y. for the doubling period, using 50 cataclysms, each killing-out one-third of the existing species of flowering plants. This might have been regarded as possible before the time of Lyell, although even then a sequence of cataclysms at regular intervals of two million years would have been suspect; with the known geological record for the Cenozoic both the number and the regularity, as well as the extent, of these hypothetical cataclysms become impossible.

There seems to be no other possible and reasonable explanation of the rectilinear increase of K with time, so that the normal death of species from the senescent sterility of old age may be taken temporarily as a suitable explanation of the curvature of the BAT curve.

It is very natural, even on general grounds, to compare the species, as a particular organisation of living matter, with the individual as a special sample of this particular organisation of living matter. In the human race senescence may be considered to begin after 70 and continue until some organic or other disease brings about death; but if the individual escapes all infection, accidents, and organic disease, his death at an age approaching or over 100 years is taken as completely natural and not due to external factors except in a very subsidiary sense. The preservation of the individual at that age requires rather special conditions. Death of the human individual is ultimately due to senescence restricting the range of conditions under which the individual can continue to survive; but very many individuals succumb to the effects of external causes, and the average life of individuals is much lower than the possible maximum. With species of flowering plants further details indicate that the average life-time is very close to the maximum. External circumstances, such as geological cataclysms and biological diseases, can kill off individuals; but when once a plant species is established over a reasonably wide area, the cataclysm or disease must be very large or widespread before all the individuals of the species will be killed out. The force of this argument may be reduced by a few known cases, especially among animals, but it becomes overwhelming for plants when one considers that throughout geological time species have been disappearing with great regularity and in all parts of the world. There is some evidence that species of Compositæ may have survived longer, or doubled in number more quickly, in South Africa than elsewhere (Small and Johnston, 1937), but apart from this area, and possibly the Brazilian highlands, there is no sign of any break in the general rule.

Other evidence for normal death as the cause of the disappearance of at least 99 per cent. of species of Angiosperms is obtained when we consider the residual increase in number of species when the K factor is acting, but this is too complex a problem to form part of the present contribution.

Returning to the quantitative method, we may now consider the possible consequences of normal death of species in flowering plants. If we follow the doubling of species-number and consider the number of new species actually arising in each doubling period, we get, for Basic Doubling,

Totals . . .	1	2	4	8	16	32	64	128	256	512	1024	2048	4096	8192
Origins . . .	1	1	2	4	8	16	32	64	128	256	512	1024	2048	4096

Now if we take the changes which may be introduced by species dying a normal death after a certain number of doubling periods, we get deaths and totals thus:—

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Now if we take the changes which may be introduced by species dying a normal death after a certain number of doubling periods, we get deaths and totals thus:—

Deaths after 6 doubling periods	..	..	..	..	..	..	..	1	1	2	4	8	16	32
give totals . .	1	2	4	8	16	32	64	127	253	504	1004	2000	3984	7936
while deaths after only 2 doubling periods . .	..	..	..	1	1	2	3	6	11	21	39	73	136	254
give totals . .	1	2	4	7	13	24	45	84	157	293	547	1021	1906	3558

It becomes obvious that the normal death of species, even after a relatively short life, might alter the apparent age, as measured by doubling periods, only by one or two units of Dp-age, and that this effect alone would not bend the "Dp-age to time" relation to anything like the BAT curve. We must be prepared to go farther and consider the senescence in genera along the lines laid down by Bentham (1873, p. 481; see Small, 1919, pp. 189–190). Bentham says: "The result of the best-founded opinions on this subject which to my knowledge have been propounded is that a race of plants, be it tribe or genus or species, in its period of full vigour, is . . . numerous and varied in subordinate races. . . . On the other hand, a race in a state of decay is represented by subordinate races . . . of restricted areas, and requiring for their preservation special climatological or other physical conditions, and consequently comparatively few in number." Since Bentham's time the rise and decay of genera has been traced so often in the geological history of animals that it has become one of the outstanding problems of evolution.

Given that species die a normal death after a limited life-time, we can now suggest that, just as the production of new individuals within species gradually ceases, so within genera the production of new species gradually ceases. By taking the species origins as following a series of 1 1 2 4 8 16 13 0, instead of 1 1 2 4 8 16 32 64, etc., and tabulating the results with about seven genera over a period of 36 m.y., with a doubling period of 2 m.y. and a normal life-time of 12 m.y., a preliminary stage has been reached where there is a level extinction of 16·6 per cent. in each doubling period. The residual doubling in species-number for each 12 m.y. has also been worked out, and the rise and decay of genera may be considered as following a course of this kind, which, combined with species deaths, would completely account for the linear relation of K values to time. This is all completely worked out in a later contribution.

This decrease of species-production by genera, after five doubling periods, would serve as some explanation of the observed excess of calculated over observed frequencies in genera of more than forty species, which was found in Compositæ (Small and Johnston, 1937, Table III), but the problem of the three large genera still remains. The normal or typical history of a genus is part of a later contribution.

The bearing of the above conclusions upon Yule's "Mathematical Theory of Evolution" (1924) should be made quite clear. In correspondence Yule takes quite a strong view of the matter thus: "If you are right, as of course you may be, in your assumption of a definite law of mortality for species, I am quite definitely wrong in my theory of the frequency distributions, and the theory requires reconstruction, your assumed law of mortality being of a simple kind that would permit of this" (Letter, February 1, 1936).

Since Yule considered the effects of continuous dying-out and of cataclysmic killing—going as far as 100 cataclysms in 100 million years, each cataclysm killing out one-third of existing species of flowering plants (*op. cit.*; p. 81)—and occupied about 13, or 20 per cent., of his 67 pages with this subject, he clearly did not at that time take the view that species-death would invalidate his main formulæ, which are expounded within the limits of the same memoir. The formulæ in question are, however, based upon frequency distributions occurring in living genera and species, as demonstrated by Willis (1922). The great majority of these genera and species are not supposed to be senescent, and the comparatively small proportion which are senescent do not markedly affect the lower categories of generic sizes with their large numbers, but begin to show in the smaller numbers of older, larger genera, as is demonstrated for Compositæ (Small and Johnston, 1937). That a large proportion of ordinary genera ultimately end abruptly in what amounts to a minor biological cataclysm is indicated above in the species-production series, and the details of this phenomenon form part of a general consideration of the significance of the reciprocals of the K values.

If the present conclusions be correct, Yule's theory, although it is fundamentally sound, requires modification by the introduction of appropriate factors for the limit-ages of species and of genera. The factor, say x doubling periods, for species limit-age would be simple, but the factor, say y doubling periods, for the decay of species-production by genera would have to be more complex. Although x will appear presently to be about 6, and y also 6 with a partially delayed action over another 6, for Angiosperms in general, and probably for the Gymnosperms with a different m.y. value, this does not necessarily apply to other groups. Therefore the factors for normal death may well vary from group to group of plants and animals, and in this case the mathematician, before presenting a reconstruction of Yule's theory, requires an analysis of the facts, along lines similar to those found for Compositæ and the Grasses, for each group considered.

Further, before the mathematician can reasonably make the assumption of normal death for species, he requires some basis for this, and also a quantitative basis for the values of x and y. The mere idea, as well as the quantitative basis, is being presented in this series of papers for the first time as more than just a somewhat improbable possibility. The general idea of normal death of species, combined with normal decay in species-production for genera, occurs occasionally in the literature, on account of the fact that, practically without exception, all species and most genera appear to die out in the fossil record, which is full of unexplained examples of the rise and decay of genera or lineages (Lang, 1919, and Crampton, 1901). The idea of normal death of species has always been only a vague possibility, which has been rejected because of the lack of precise evidence; but the nature of the required evidence appears to have been generally neglected. Recent publications give some attention to the general phenomena of sterility. McLean Thompson (1929, p. 41) notes that 28 out of 400 genera in the Leguminosæ show reduction to one seed per legume, while in another 101 genera there may be only one, two, or a few ovules per legume. M. de Wildeman (1936) concludes his extensive memoir with the statement, "Nous avons essayé de montrer qu'il existe chez les espèces végétales une tendance vers la stérilité."

If the normal life-time of a species in Angiosperms is about 12 m.y., as will appear presently, the senescence of a species could easily spread over half a million years or more. In such a case the only critical evidence available would be the facts of advancing sterility and of advancing specialisation of habitat in a relatively small proportion of species. Both these sets of facts are well known as reasonably common phenomena, but they do not appear to have been studied from the point of view of actual senescence in species and genera.

CONCLUSION AND SUMMARY.

Placing Compositæ Dp-ages in relation to a time-scale, it is found that the apparent length of the doubling period in years (Dp-age unit) increases directly with time.

Corresponding values from the BAT curve show a closely similar rectilinear relation to time.

This increase in length is taken as due to the effect (K) of a factor depressing the apparent Dp-age to a degree which is directly proportional to time or to the age in years of the group of genera considered.

From the rectilinear increase with time shown by the K values, it is concluded that species have a limited life-time and die a normal death, and, further, that most genera have a natural life-period and show a normal decay in species-production which, combined with normal death of species, leads to a normal extinction of most genera.

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III.—Quantitative Evolution. V. The Free and Apparent Dp-ages of Compositæ.

By **Professor J. Small,** D.Sc., Department of Botany, Queen's University, Belfast. (With Two Figures.)

(MS. received September 11, 1937. Read December 6, 1937.)

THE average ages in doubling periods (Dp-ages) of the tribes and sub-tribes of Compositæ have been collated with geological time (Small, 1937, Q.E. II), but the Dp-ages of individual tribes and sub-tribes show considerable variation within each of the geological periods. When plotted as Dp-ages against a time-scale the tribes and the sub-tribes show rather scattered positions, and the sub-tribes within each tribe follow rather zigzag lines instead of being points on a straight line for each tribe.

It has, however, been shown (Small, 1938, Q.E. IV) that for each geological period there is an average depression of Dp-age by a factor (K), the value of which for each period has been determined. The values of the depressant K for the mid-points of the various periods, with the Arctotideæ and Helenieæ taken as of Lower Pliocene origin, are as follows: Pliocene K = 1·13 around a 6 m.y. mid-point; Miocene K = 2·15 around 18 m.y.; Oligocene K = 3·16 around 32 m.y.; Eocene K = 4·49 around 49 m.y.; Paleocene and Late Cretaceous as "Earlier" K = 5·87 around 70 m.y.

The apparent Dp-ages plotted against time yield a peculiar curve, the BAT curve (Small, 1937, Q.E. II), and in order to obtain ages which should be more or less on a straight line of progress it is necessary to multiply each apparent Dp-age, as calculated originally, by the K value for the period of origin for each tribe and sub-tribe. In this way we obtain Dp-ages in terms of the free doubling period of 2 m.y., instead of in terms of the apparent doubling periods, the units of which get progressively longer as we pass backwards in time of origin. The original Dp-ages may now be termed "apparent Dp-ages," and the new values obtained by the use of the K correction may be termed "free Dp-ages" and considered as being nearer a linear measure of the ages of the groups concerned. When these calculations are carried out as in Table I, a number of sub-tribes within some of the tribes can be grouped because they have their origin with the same sub-period. A careful study of the free Dp-ages as given in Table I shows the original seriation of Dp-ages in a slightly improved condition. The exceptions to seriation have been described in a previous contribution (Small and Johnston, 1937).

TABLE I.

FREE DP-AGES IN COMPOSITAE

SUBTRIBES	$T_{APP.}$	×K	T_{FREE}	AVER.	TIME
SENECIONIN.	8·41	5·87	49·37		C.
LIABINÆ	3·89	2·15	8·36		L.M.
TUSSILAG.	2·66	"	5·72		U.M.
OTHONNINÆ	2·60	1·13	2·94		M.P.
EU-GNAPH.	4·27	5·87	25·06		C.
PLUCHEINÆ	4·02	2·15	8·64	7·37	L.M.
FILAGININÆ	2·84	"	6·11		L.M.
TARCHONAN.	2·17	1·13	2·45		L.P.
HELICHRYS.	3·09	2·15	6·64		M.M.
RELHANIINÆ	2·01	1·13	2·27	2·13	M.P.
ANGIANTH.	1·77	"	2·00		M.P.
VERBESIN.	4·30	4·49	19·31	18·94	L.E.
COREOPSID.	4·135	"	18·57		L.E.
GALINSOG.	3·915	2·15	8·42	7·50	L.M.
MADIINÆ	3 69	"	7·93		"
MELAMPOD.	2·86	"	6·15		"
AMBROSIINÆ	2·82	"	6·06	5·65	M.M.
MILLERIINÆ	2·33	"	5·01		"
ZINNIINÆ	2·27	"	4·88		"
LAGASCEINÆ	—		—		U.M.
PETROBIINÆ	—		—		L.P.
HOMOCHROM.	5·36	4·49	24·08		M.E.
HETEROCHROM.	5·20	"	23·34		U.E.
CONYZINÆ	4·06	3·16	12·82		U.O.
BACCHARID.	3·70	2·15	7·96	7·40	M.M.
BELLIDINÆ	3·185	"	6·85		M.M.
GRANGEINÆ	1·65	"	3·55		U.M.
CHRYSANTH.	6·95	4·49	31·20	34·05	U.E.
ANTHEMID.	8·22	"	36·90		U.E.
CREPIDINÆ s.	6·04	4·49	27·12		U.E.
LEONTOD. s.	5·87	3·16	18·55		M.O.
CICHORIINÆ s.	3·03	2·15	6·51		M.M.
DENDROSER.	4·29	—	—		U.M.?
NASSAUV.	5·70	3·16	18·01		L.O.
ONOSERID.	7·65	"	24·17	21·60	M.O.
GERBERINÆ	6·02	"	19·02		M.O.
GOCHNATIINÆ	5·52	"	17·44		U.O
BARNADES.	—	—	—		—

SUBTRIBES	$T_{APP.}$	×K	T_{FREE}	AVER.	TIME
INULINÆ	6·60	3·16	20·86		M.O.
BUPHTHAL.	2·07	"	6·54		U.O.
(CYNAREÆ)	4·93	2·15	10·60		L.M.
ATHRIXIINÆ	3·09	"	6·64		U.M.
RELHANIINÆ	2·01	1·13	2·27		M.P.
CENTAUR.	6·17	2·15	13·27	12·34	L.M.
CARDUINAE	5·31	"	11·42		L.M.
CARLININAE	3·50	1·13	3·73		L.P.
ECHINOPSID.	—	—	—		"
AGERATINÆ	4·85	2·15	10·43		M.M.
ADENOSTYL.	3·50	"	7·82		U.M.
PIQUERIINÆ	3·23	1·13	3·64		L.P.
VERNONIINÆ	3·61	2·15	7·79		U.M.
LYCHNOPHOR.	2·87	1·13	3·24		L.P.
(HELENIEAE)	3·20	1·13	3·62		L.P.
ARCTOTIDIN.	2·45	1·13	2·77		L.P.
GORTERIINÆ	2·25	"	2·54		M.P.
GUNDELIINÆ	<1·0				U.P.
(CALENDUL.)	2·43	1·13	2·75		L.P.

TRIBES	$T_{APP.}$	×K	T_{FREE}	AVER.	TIME
SENECION.	7·26	5·87	42·63	34·96	C.
GNAPHAL.	4·65	"	27·30		PAL.
HELIANTH.	3·86	4·49	17·33	24·53	L.E.
ASTEREAE	5·06	"	22·72		M.E.
ANTHEMID.	7·04	"	31·59		U.E.
CICHORIEAE	5·90	"	26·49		U.E.
MUTISIEAE	6·14	3·16	19·41	16·0	L.O.
INULEAE	3·99	"	12·60		U.O.
CYNAREAE	4·93	2·15	10·60	8·88	L.M.
EUPATORIEÆ	3·86	"	8·30		M.M.
VERNONIEAE	3·595	"	7·73		U.M.
HELENIEAE	3·20	1·13	3·62	3·01	L.P.
ARCTOTIDEÆ	2·355	"	2·66		L.P.
CALENDUL.	2·43	"	2·75		L.P.

The free Dp-ages of the sub-tribes can now be plotted against time as in fig. 1, using mid-points for subdivisions of periods, as 6 and 9 for Middle and Lower Pliocene; 13, 17·5, and 22·5 for Upper, Middle, and Lower Miocene; 26, 32, and 35 for Upper, Middle, and Lower Oligocene; 42, 47·5, and 55 for Upper, Middle, and Lower Eocene; 65 for Paleocene, and 70 for very Late Cretaceous. Then it becomes obvious that in most tribes the sub-tribes are arranged in a rectilinear fashion, more or less along straight lines which tend to a central grouping. In other words, the free Dp-ages vary directly with time, as would be expected. There are two tribes, the Helenieæ and Anthemideæ, where all the sub-tribes have origin in the same sub-period, and the Calenduleæ with no sub-tribes; these are given as points. Other sub-tribes within tribes which arise in the same sub-period are averaged, to reduce the number of points in the graphs.

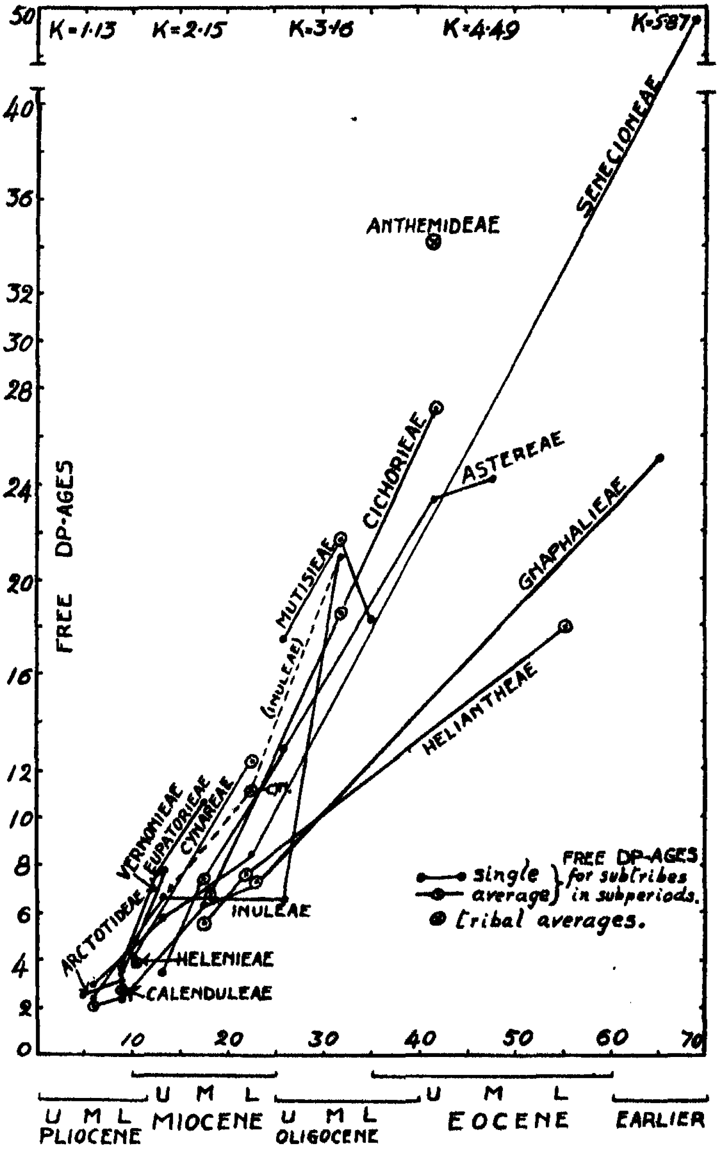

FIG. 1.—Free Dp-ages of sub-tribes in Compositæ.

There are also two exceptions to the general rectilinear arrangement. The Buphthalminæ introduces a large angle in the line of the Inuleæ (ltd), but if the derivative Cynareæ is taken as being in this line instead of the much smaller group, then the tribal age (marked CYN, fig. 1) lies upon the Inuleæ line as dotted in the figure. The other exception is the Mutisieæ, where the apparently primitive Nassauviinæ has a free Dp-age value which is low for its position in relation to other sub-tribes in the Mutisieæ. The Gnaphalieæ line and the Heliantheæ line still remain divergent, below the central grouping of all the other tribes.

When the free Dp-ages of the tribes are plotted against time in the same way (fig. 2), it becomes quite obvious that most of the tribes are grouped around a diagonal which stretches from the Calenduleæ to the Senecioneæ. The relative positions and free Dp-ages fit very closely, with certain exceptions. The Heliantheæ, Gnaphalieæ, and Astereæ show obvious divergences, but we have now reached a stage where we can measure the divergences as simple proportions of the calculated values.

If we take the statement, that "the tribes of Compositæ have arisen as a series in time with the Senecioneæ first or oldest and the Calenduleæ last or youngest," as the hypothesis to be tested, the other tribes should be arranged in a rectilinear sequence between these two points. We can calculate for each tribe the approximate free Dp-age which corresponds to its position in time with relation to the straight line of time sequence in origins. This is done by means of verticals which cut the line at the theoretical points. The original of fig. 2 being on a centimetre scale, the free Dp-age can be obtained to the first decimal place. The observed free Dp-ages are given in Table I. From these and the theoretical free Dp-ages determined as above, we can obtain the simple proportion of divergence as x/m, where x is the divergence and m is the theoretical value for the free Dp-age of each tribe.

TABLE II.

Tribes.	Free Dp-ages. Theoretical, m.	Observed.	Divergence, x.	x/m.
Calenduleæ	2·75	2·75	0	0
Arctotideæ	3·0	2·66	·34	·113
Helenieæ	3·6	3·62	·02	·006
Vernonieæ	6·8	7·73	·93	·137
Eupatorieæ	8·4	8·30	·1	·012
Cynareæ	12·0	10·60	1·4	·117
Inuleæ (ltd.)	14·6	12·60	2·0	·137
Mutisieæ	20·6	19·41	1·19	·058
Cichorieæ	25·2	26·49	1·29	·051
Anthemideæ	26·1	31·59	5·49	·210
Astereæ	29·0	22·72	6·28	·216
Heliantheæ	34·2	17·33	16·87	·493
Gnaphalieæ	40·9	27·30	13·6	·332
Senecioneæ	42·63	42·63	0	0

While the simple proportional divergence, x/m, for the Astereæ and Anthemideæ may be considered relatively small, the divergences for Heliantheæ and Gnaphalieæ would appear to be really significant. Reference to the last column in Table II will show that the Heliantheæ have a simple proportional divergence of about one-half, while the divergence for Gnaphalieæ is about one-third. The last column in Table II

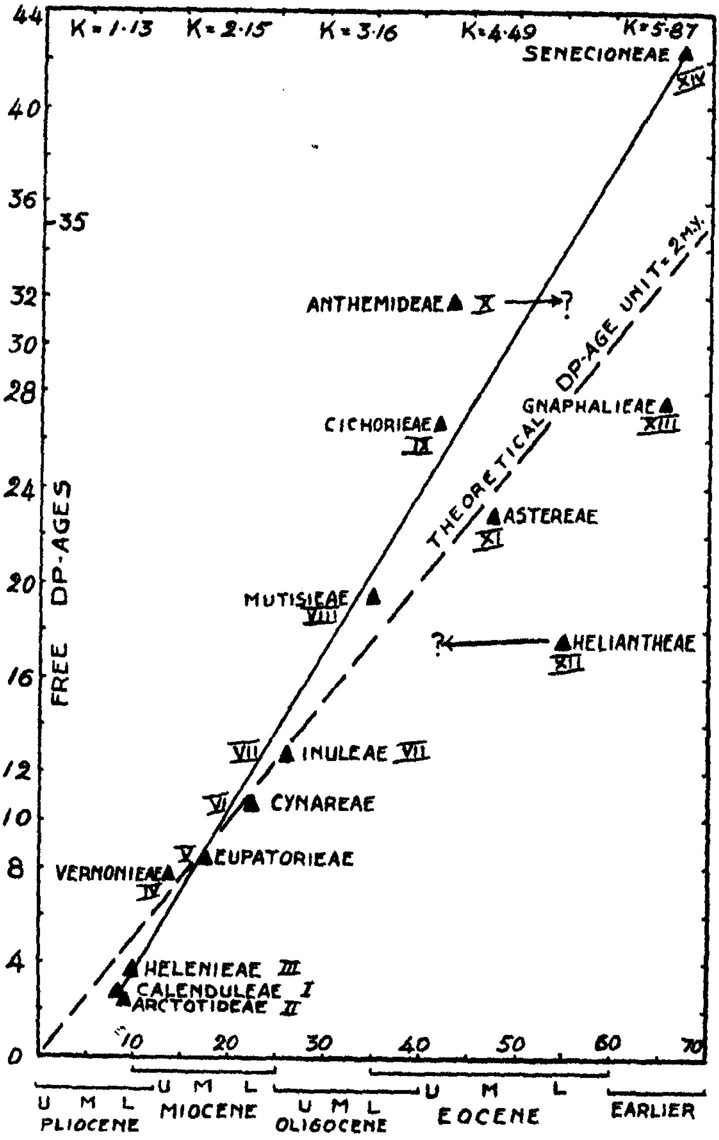

Fig. 2.—Free Dp-ages of tribes in Compositæ.

helps to emphasise the fact that, apart from the last two tribes mentioned, the observed points lie very nearly in a straight line time sequence between Senecioneæ and Calenduleæ.

Thus we reach a stage where, by means of Yule's formulæ for the determination of "apparent" Dp-ages (Small and Johnston, 1937) and the modifications introduced in consequence of the discovery of the BAT curve (Small, 1937–8, Q.E. II–IV), the evolutionary history of a group, as deduced from morphological and other data, can be tested quantitatively from quite a different angle and using quite different data. Further, we find, as a result of the quantitative testing, a confirmation of the general history of Compositæ as previously elaborated—with two probable exceptions in the cases of the Heliantheæ as a whole—and of the arrangement of sub-tribes within the Mutisieæ, together with a possible exception in the Gnaphalieæ.

THE POSITION OF THE HELIANTHEÆ.

It is suggested in fig. 2 that the Upper Eocene rather than the Lower Eocene would be a more appropriate time of origin for this tribe, and a case could be argued for placing the Heliantheæ between the Astereæ and Cichorieæ in the evolutionary sequence of tribes.

The Heliantheæ has been regarded as "no doubt the most primitive tribe of the family" (Hutchinson, 1916), following Bentham's tentative suggestions (Bentham, 1873) given as "We are led to conjecture that the primitive form of Compositæ," etc. (*op. cit.*, p. 483), and "We are led to imagine that Compositæ existed showing several important modifications" (*op. cit.*, p. 483). These conjectures and imaginings are given by Rendle (1925, p. 611) as "a more philosophical explanation" than the present author's views. Rendle (*loc. cit.*) also states that "the genus *Senecio* represents a stage of specialisation well advanced."

The main apparently primitive features of the Heliantheæ are the elongation of the receptacle and the foliaceous receptacular scales which occur in some genera. These are characters of the inflorescence rather than the flower, and much easier to observe than the details of actual floral structure. The florets are definitely of quite an advanced type in their styles and aristate pappus as fused setæ. The main point at issue is the derivation of the capitulum from a spike giving the Helianthoid inflorescence, or from an umbel giving the Senecionoid inflorescence as primitive. The discoid or rayed structure is of very minor importance, since Trow (1916) indicates clearly that radiateness of the capitulum is, at least in *Senecio vulgaris*, a simple Mendelian dominant and not a character which is likely to develop gradually.

So far as the writer is aware, no one who has studied inflorescences as such has supported the view that the capitulum arises from a condensed spike. The origin of the capitulum from an umbel has been argued at length (Small, 1919), and these arguments have never been met. They have been accepted by Yapp (1923), and confirmed from umbellate proliferated heads of *Crepis* and *Hypochœris* (Collins, 1921). Lindley (1839) had already suggested this mode of origin for the capitulum. Parkin (1914) makes only a passing reference to the subject, but he gives a diagram (*op. cit.*, pl. 18) in which the spike is regarded as a side line and the head as derived from the simple raceme through the corymb and the umbel. Masters (1869) records umbellate proliferations in *Senecio*, *Hypochœris*, etc.

Senecio is simple throughout its floral structure, and if the umbel origin of the capitulum is accepted, the involucre and receptacle of this genus are seen to be simple because they are primitive, and not on account of a quite hypothetical reduction from a Helianthoid type. The general views expounded in *The Origin and Development of Compositæ* were specially considered at a meeting by J. M. Greenman, the monographer of American Senecios, and his colleagues; and the writer's "viewpoint concerning the Compositæ was very well received" (Letter, March 18, 1920).

With the umbel origin of the capitulum and the primitive position of the Senecioneæ both supported by actual workers on the family, the derivative advanced position of the Heliantheæ indicates a later origin within the time scheme of the family. Nevertheless, there are possibilities of extensive generic senescence giving the low value for Dp-age in this tribe, and possibly also in the Gnaphalieæ and Astereæ. Therefore it is considered better to leave the original scheme as it is in the meantime, because it may ultimately be more informative to have significant divergences than to have a phylogenetic scheme which is re-arranged in any decided degree to fit the facts of Dp-age values as now calculated.

CONCLUSIONS AND SUMMARY.

The depressant effect of dying-out upon the "apparent" Dp-ages of groups is used quantitatively, as the average K values for periods, in calculation of the "free" Dp-ages (or ages in doubling periods of uniform 2 m.y. length) for each tribe and sub-tribe in Compositæ.

These free Dp-ages are tabulated (Table I) and presented as graphs against a time-scale, showing all the sub-tribes within tribes as approximately rectilinear sequences in time (fig. 1).

The free Dp-ages of tribes are similarly presented as points around a straight line from Calenduleæ to Senecioneæ in a time sequence (fig. 2).

The proportional divergences, from a rectilinear graduation or sequence in time, are calculated and shown to be relatively insignificant, except in the cases of the Heliantheæ and Gnaphalieæ.

The position of the Heliantheæ is reviewed, mainly from the viewpoint of the origin of the capitulum from the umbel and the relatively advanced floret structure in the tribe, but it is considered that one or two significant divergences may finally be more informative as "exceptions proving the rule," and the original phylogenetic arrangement is left unmodified.

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(*Issued separately January* 27, 1938.)

IV.—Quantitative Evolution. VI. Further Deductions from the BAT Curve. By **Professor J. Small,** D.Sc., Department of Botany, Queen's University, Belfast. (With Three Figures.)

(MS. received September 11, 1937. Read December 6, 1937.)

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PREVIOUS communications have established the formula for the BAT curve as $-\text{Dp}.k+n.d=t_k \,.\, 2^n$, where k is a constant Dp-age, d is a constant difference of Dp-age, t_k is the time value in m.y. at the Dp-age k. For Compositæ (Small, 1937, Q.E. II) and apparently also for the Grasses (Small, 1937, Q.E. III) $k=0{\cdot}6$, $d=0{\cdot}9$, $t_k=1{\cdot}09375$ m.y.

I. FURTHER POINTS ON THE BAT CURVE.

From the above formula—
with T the time in m.y. known, Dp-age $=k+n.d$,

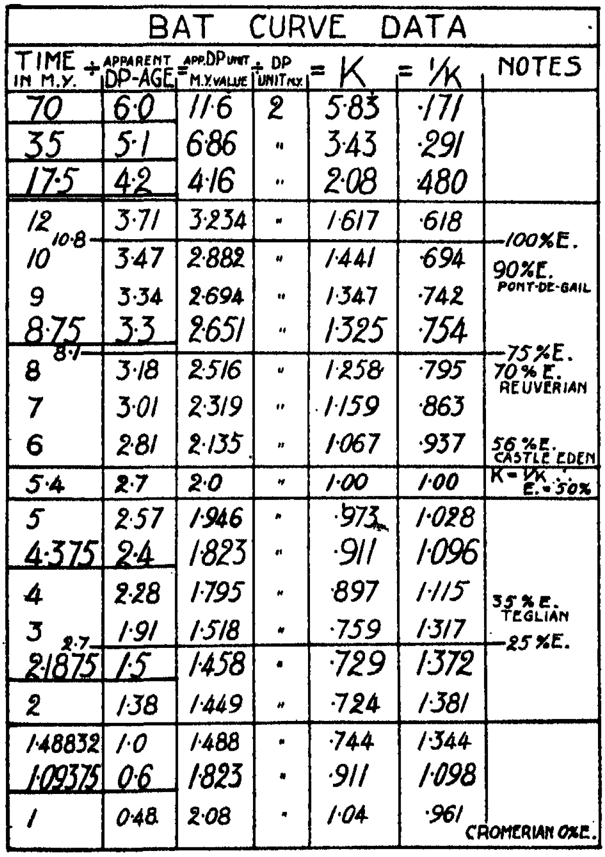
$$\text{where } n=\log\frac{\text{T}}{t_k}\cdot\frac{1}{\log 2};$$

with Dp-age, or age in doubling periods known,

$$\text{T}=t_k\,.\,2^n, \qquad \text{where } n=\frac{\text{Dp-age}-k}{d}.$$

Any point on the BAT curve can, therefore, be calculated, either for time as geological time on the scale adopted (Small, 1937, Q.E. II), or for any apparent Dp-age which may be observed in any group to which the above values of the constants apply. These calculations have been made for a number of points within the last 12 m.y., a period which has a special interest. They will be found in Table I, and can be used for further deductions from the BAT curve.

TABLE I.



BAT CURVE DATA

TIME IN M.Y.	÷ APPARENT DP-AGE	= APP. DP UNIT M.Y. VALUE	÷ DP UNIT M.Y.	= K	= 1/K	NOTES
70	6·0	11·6	2	5·83	·171	
35	5·1	6·86	"	3·43	·291	
17·5	4·2	4·16	"	2·08	·480	
12	3·71	3·234	·	1·617	·618	
10·8						100%E.
10	3·47	2·882	"	1·441	·694	90%E. PONT-DE-GAIL
9	3·34	2·694	"	1·347	·742	
8·75	3·3	2·651	"	1·325	·754	
8·7						75%E.
8	3·18	2·516	"	1·258	·795	70%E. REUVERIAN
7	3·01	2·319	"	1·159	·863	
6	2·81	2·135	"	1·067	·937	56%E. CASTLE EDEN
5·4	2·7	2·0	"	1·00	1·00	K = 1/K ∴ E. = 50%
5	2·57	1·946	·	·973	1·028	
4·375	2·4	1·823	"	·911	1·096	
4	2·28	1·795	"	·897	1·115	35%E. TEGLIAN
3	1·91	1·518	·	·759	1·317	
2·7						25%E.
2·1875	1·5	1·458	·	·729	1·372	
2	1·38	1·449	"	·724	1·381	
1·48832	1·0	1·488	·	·744	1·344	
1·09375	0·6	1·823	·	·911	1·098	
1	0·48	2·08	·	1·04	·961	CROMERIAN 0%E.

II. THE YEAR VALUE OF THE DP-AGE UNIT.

This value has been taken as approximately 2 m.y. in previous contributions (Small, 1937–8, Q.E. II–V). It might be considered that the true m.y. value of the Dp-age unit should be taken as the time value (1·49 m.y.) where the Dp-age appears as 1·0. This is certainly the lower limit, but it will be observed that below 2 m.y. some irregularities appear in the sequences of values, and since the observed points for the BAT curve formula are at 70, 35, 17·5 m.y., and the curve is calculated from past to present, there is a certain doubt as to the strict verisimilitude of the lower time values. For example, the length of the Pleistocene is given in Schuchert and Dunbar (1933, p. 432) as "all students of the Pleistocene history now agree that the entire duration of the Pleistocene was at least several hundred thousand years, it probably exceeded a million." If we now bring in post-Pliocene time as about half a million years, this may be added to the 1·49 m.y. at Dp-age 1·0 to give again something very near the unit value of 2 m.y. which has been used.

Again considering the observed average Dp-age of 2·66 for Pliocene (Small and Johnston, 1937, p. 47); this is for the Pliocene with a length between 10 and 12 m.y., the mid-point taken being 6 m.y., but the average of the estimated lengths is 11 m.y., giving a mid-point at 5·5 m.y., which corresponds closely to the 5·4 m.y. of Table I, where the calculated apparent Dp-age is 2·7 instead of the observed 2·66, and where the year value of the Dp-age unit is 5·4/2·7 or 2·0 m.y. instead of 5·5/2·66 or 2·08 m.y.

Since the Pliocene tribal average Dp-age is the lowest observed point, and since various disturbing elements come into the calculations for lower points, it appears to be safer to adhere to the previously used value for the Dp-age unit, namely, 2·0 m.y., which may really be 2·08 m.y. if the observed points are quite accurate. There is no reason to suppose that these points are very accurate, and the close agreement between observed points and points calculated from the BAT curve is a further confirmation of the closeness of fit of the BAT curve to the observed data.

It is, for example, definitely encouraging to find that when we require 0·51 m.y. of post-Pliocene time to give the 2·0 m.y. for Dp-age 1·0, the general estimate of geologists lies between several hundred thousand and over one million, while the well-known Pleistocene geologist, Professor J. K. Charlesworth, gives verbally a rough estimate of half a million years.

III. THE K VALUES AND THEIR RECIPROCALS.

The K values show a progressive increase from 3 to 70 m.y. (Table I, col. 5). The reciprocals, 1/K, of these values show a progressive decrease from 3 to 70 m.y. (Table I, col. 6). When these K values are graphed (fig. 1) it is seen that they increase almost directly with time; there is a slight divergence which is distinct below 12 m.y. When the 1/K values are graphed (fig. 1) it becomes clear that they decrease with time along something like an exponential curve.

There are various deductions which may be made from these two sets of values, and the first concerns the point at which K and 1/K are both equal to 1·0 at 5·4 m.y.

If K is a measure of the effect which dying-out of species and genera has had upon the apparent Dp-age of a group, then its reciprocal 1/K is a measure of the extent to which apparent Dp-age has not been affected by dying-out. When these effects are equal we get the effects of progressive increase in species-number and of dying-out equal, so that we may take backward extinction of existing species as 50 per cent. at 5·4 m.y. Briefly, if we take K as the extinction factor and 1/K as the non-extinction factor, there is 50 per cent. of each when K = 1/K at 5·4 m.y. It is shown below (Sect. IV and VI) that percentage backward extinction of existing species proceeds along a straight line, so that with 50 per cent. at 5·4 m.y. we should expect at least 99 per cent. at 10·8 m.y. This enables us to deduce the average life-time of a species as not less than 10·8 m.y.

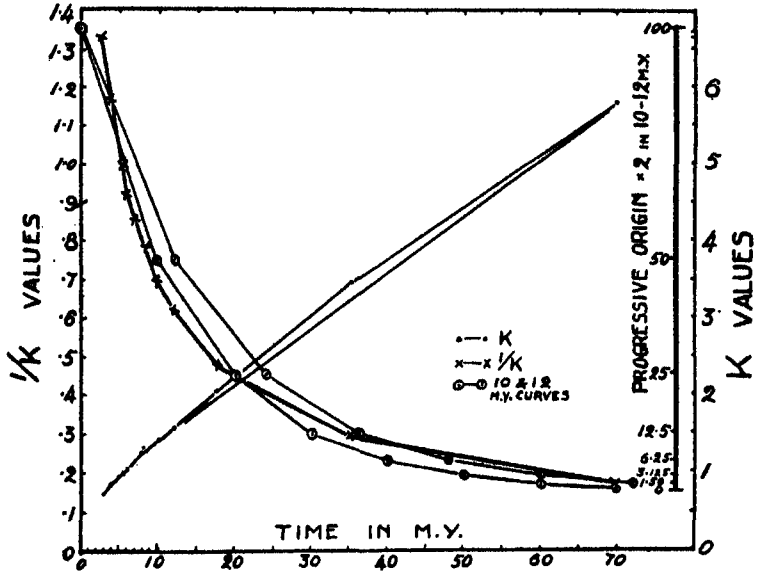


FIG. 1.—K and 1/K values for Compositæ.

A second deduction is made by fitting exponential curves with 10 m.y. and 12 m.y. doubling periods to the ends of the 1/K curve (fig. 1). These are curves of progressive increase in species-number, while the 1/K curve is a measure of the increase in the approximation of apparent Dp-age values to free Dp-age values. It will be shown below that Dp-age between 2·66 and 6 varies nearly directly as average number of species per genus, rather than along a simple geometrical progression, other things being equal (Sect. V). We therefore take the 1/K curve in fig. 1 as a third curve of progressive increase in species-number, and find that it approximates closely to the other two curves. With a 12 m.y. doubling period the lower part of the 1/K curve is fitted very closely, while with a 10 m.y. doubling period the upper part of the 1/K curve is fitted very closely. Therefore, we can make a second deduction to the effect that, after the influence of dying-out has been eliminated or allowed for, there is an average residual increase in species-number which shows a doubling period of 10 m.y to 12 m.y.

Before going on to further deductions the two points to be demonstrated in connection with the above conclusions have to be considered (Sect. IV and V).

IV. SUB-TOTAL EXTINCTION.

With the year value of the Dp-age checked as approximating fairly closely to 2 m.y., we can consider actual existing species. Since the oldest of these species cannot be of greater age than the maximum life-time of a species, and since these species are all living, we may assume for the moment that no deaths are taking place. Then with a free doubling period of 2 m.y. we would expect to find that 50 per cent. of the living species of a group were not in existence 2 m.y. ago; similarly, there would be only 25 per cent. existent 4 m.y. ago; and so backwards through 12·5 per cent. at 6 m.y.; 6·25 per cent. at 8 m.y.; 3·125 per cent. at 10 m.y.; 1·5625 per cent. at 12 m.y.; 0·781 per cent. at 14 m.y. With sub-total extinction defined as the disappearance of about 99 per cent., this simple consideration shows that 98·4 per cent. of existing species of Compositæ (and probably of Angiosperms in general) were not in existence 12 m.y. ago; so that there is a sub-total extinction of existing species at or near the base of the Pliocene.

These percentages for apparent backward extinction give a hollow curve of "progressive origins" similar to those in fig. 1, but with a 2 m.y. doubling period. It should be noted carefully that these percentages are calculated as percentages of the total number of now existing species in a group. Lyell's curve for survivals of existing species of "shells" yields percentage points as Pleistocene 100–90, Pliocene 90–50, Miocene 40–20, Oligocene 15–10, Eocene 5–1, Paleocene 0 (Schuchert and Dunbar, 1933, p. 384). These were also calculated as percentages of the total number of now existing species in a group, and show the same form of curve, with 11 m.y. as the approximate value of the doubling period. The significant data are 6·25 per cent. at 44 m.y.; 12·5 per cent. near 33 m.y.; 25 per cent. at 22 m.y.; 50 per cent. near 11 m.y.; 100 per cent. now. Lyell's shell data are now rather suspect, but his curve may serve as an example of a curve of progressive origin which lies between the two given in fig. 1, with doubling periods of 10 m.y. and 12 m.y. respectively.

There is a second method of calculating these percentages, where the percentage is taken as the proportion of now existing species which occurs in the total known flora at any given point in time. This method takes into consideration not only species which are now living, but also species which were living and are now dead. This method was used by Mrs Clement Reid, who gave a table (Willis, 1922, p. 144) of percentages of extinct species belonging to the Chinese-North American Association of Plants in the West European Pliocene at successive periods. The percentages are given as approximate, and the highest figure (90 per cent.) is supported by data from Nathorst's list, which gives 89 per cent. for a similar period in a Japanese deposit. Mrs Reid's data for the percentage of extinct species are 0 for Cromerian (top of Pliocene); 35 for Teglian (Upper Pliocene); 44 for Castle Eden (Middle Pliocene); 70 for Reuverian (low down in Lower Pliocene); 90 for Pont-de-Gail (base of Pliocene).

When we consider these as proportions of partially extinct floras, and by subtraction obtain the percentages of now living species over living plus dead species of that association, which occur at the various levels, we get 100 per cent. at the top of the Pliocene; 65 per cent. for Teglian or Upper Pliocene; 56 per cent. for Castle Eden or Middle Pliocene; 30 per cent. for Reuverian or Lower Pliocene; and 10 per cent. for Pont-de-Gail or base of the Pliocene.

With the Pliocene taken as 10·8 m.y. we get 5·4 m.y. as the mid-point of Middle Pliocene, 2·7 m.y. as the mid-point of Upper Pliocene, 8·1 m.y. as the mid-point of Lower Pliocene, and 10 m.y. as near the base of the Pliocene. Following Reid's placing of the named deposits, and placing these at approximate positions on the time-scale (Table 1, col. 7) we get a very close approach to a rectilinear percentage extinction for the Pliocene. The 35 per cent. at Upper Pliocene is somewhat divergent, unless the Teglian is taken as between 3 m.y. and 4 m.y., but the other four points are in close agreement with the straight line of extinction, and in any case the Reid points do not in any way resemble points on a hollow curve of progressive origins. This is on account of the presence in the data of species which are now extinct.

V. THE LIFE-TIME OF A SPECIES.

Using the rectilinear backward extinction, supported by Reid's data as above, we find that it reaches 100 or 99 per cent. extinction about 10·8 to 12 m.y., the exact extinction point depending on the placing of the deposits. If we take Pont-de-Gail as at 10·8 m.y., 99 per cent. extinction is extended to about 12 m.y.

The basis of rectilinear backward extinction, giving 10·8 m.y. as the average life-time for species in Compositæ, is therefore confirmed or supported by data from the Chinese-North American Association of Plants. But the Reid data would indicate a *maximum* life-time, for at least 99 per cent. of the Angiosperms concerned, of 10 to 12 m.y., whereas the BAT curve data give at least 10·8 m.y. as the *average* life-time. It would appear, therefore, that about 99 per cent. of species of Angiosperms attain nearly or quite to the maximum life-time.

RESIDUAL DOUBLING.—The second deduction made above involves a rectilinear increase of the average number of species per genus in relation to Dp-ages between 2·66 and 6. Taking s/g at the family value of 2·1 (Small and Johnston, 1937, p. 54), and referring to the basic tables (Yule, 1924, Table III, p. 53), we find that for Time or Dp-age values of 2, 3, 4, 5, 6, the M values (or average number of species per genus) increases thus: 3·037, 4·765, 7·248, 10·819, 15·953. It will be seen at once that these values do not increase by doubling in value for each unit increase of Dp-age. Reducing them to more easily comparable figures we get: 1·0, 1·5, 2·0, 2·5, and 3·0 for the Dp-age proportions, and 1·0, 1·56, 2·39, 3·56, and 5·24 for the proportions of M values as compared with the 1, 2, 4, 8, 16 given by a simple 2^n geometrical progression. The direct relation of M to Dp-age is fairly close for Dp-ages 2 to 4, but M begins to rise more rapidly in the region of Dp-age 5–6. The agreement is sufficiently close to a rectilinear relation, and, what is perhaps more important, the relation is sufficiently far away from a simple 2^n progression to justify the interpretation of the 1/K curve as approximating to that of a curve of residual progressive increase in species-number. Thus the basis of our second deduction is shown to have a reasonable foundation, and we can proceed farther, using this curve as a curve of progressive origin giving a residual increase in species-number with a doubling period of 10 to 12 m.y.

We have already used this residual doubling period to show how, by successive halving of the 6000 species-number in the Grasses, we reach zero in Upper Cretaceous times (Small, 1937, Q.E. III). The use of 10·8 m.y. instead of 12 m.y. would bring the zero some 9 m.y. higher up, about 87 m.y. instead of 96 m.y., and this does not agree with the Dp-age of Paniceæ, which is 6·33, giving 95 m.y. as the time of origin of this nearly basal group. The 12 m.y. doubling period also agrees better with species-number calculations for the Compositæ and the Angiosperms as a whole. It also fits better into a general scheme of the life of a genus, which is considered below (Sect. VII).

VI. NORMAL DEATH OF SPECIES.

It has already been suggested that species and genera die a natural normal death from the senescent sterility of old age, and the presence of the necessary evidence of advancing sterility amongst still living genera has already been indicated (Small, 1938, Q.E. IV). Behind that suggestion lies the evidence here deduced of the majority of species in general continuing to survive up to their maximum life-time. In other words, if the ***average*** life-time of Angiosperm species in general is also the ***maximum*** life-time of Angiosperm species in general, then species are not normally killed by external agencies, but die a natural death after a definitely limited life-time.

When the average is the same as or very near the maximum there can be relatively few short life-times, while there is no evidence in Compositæ of species living longer than the maximum 12 m.y. This relation between average and maximum may not hold for some groups of animals, such as the relatively few molluscs which are used as "zone fossils," but investigation of exceptions rather than controversy on details is required in quantitative evolution.

The analogy of a human life kept free from all accidents, infection, and organic disease has already been given (Small, 1938, Q.E. IV), together with a beginning of the evidence which may be accumulated concerning senescent sterility in species and genera. This at least opens up a new field of interest, not only in advancing sterility, but also in relic endemics and cases of natural discontinuous distribution as possible evidence of normal senescence.

SIGNIFICANT DATA.—Recapitulating the data deduced from the BAT curve we have:

1. The free doubling period or Dp-age unit is very nearly 2 m.y.;
2. The normal life-time for a species is very nearly 12 m.y.;
3. The average residual increase in species-number as distinct from actual species has a doubling period of about 12 m.y.

These data apply to the Compositæ in particular, and apparently also to the Grasses and to Angiosperms in general. It is known from unpublished results that they do not apply to some groups of animals.

VII. THE LIFE-HISTORY OF A GENUS.

It has already been noted in general terms that the normal life-time of a genus of Angiosperms appears to extend over 12 to 14 doubling periods (Small, 1938, Q.E. IV, p. 20), and this would give 24 to 28 m.y. as the normal life-time for a genus. We have now reached a stage where the typical life-history of a genus, as a group of species, may be studied numerically.

It has been shown (Small, 1938, Q.E. IV) that the simple dying-out of species after 12 m.y. would have only a slight effect upon the free Dp-ages of groups of species, which would continue to double in number at a rate approaching that of free doubling without any death of species. In order to account for the shape of the BAT curve—that is, for the observed effects of dying-out on the free Dp-ages of groups of related genera—it is necessary to consider the decay of species production within the genus.

If we take free doubling along a 2^n progression we get species-number within the genus increasing thus: 1, 2, 4, 8, 16, 32, 64, 128, but if we consider each species as dying after a 12 m.y. life-time, the origins in this case are 1, 1, 2, 4, 8, 16, 32, 64; and the corresponding deaths after six doubling periods would reduce the series of origins and survivals to 1, 2, 4, 8, 16, 32, 63, 127. It becomes clear that we must consider species production as failing after about six doubling periods.

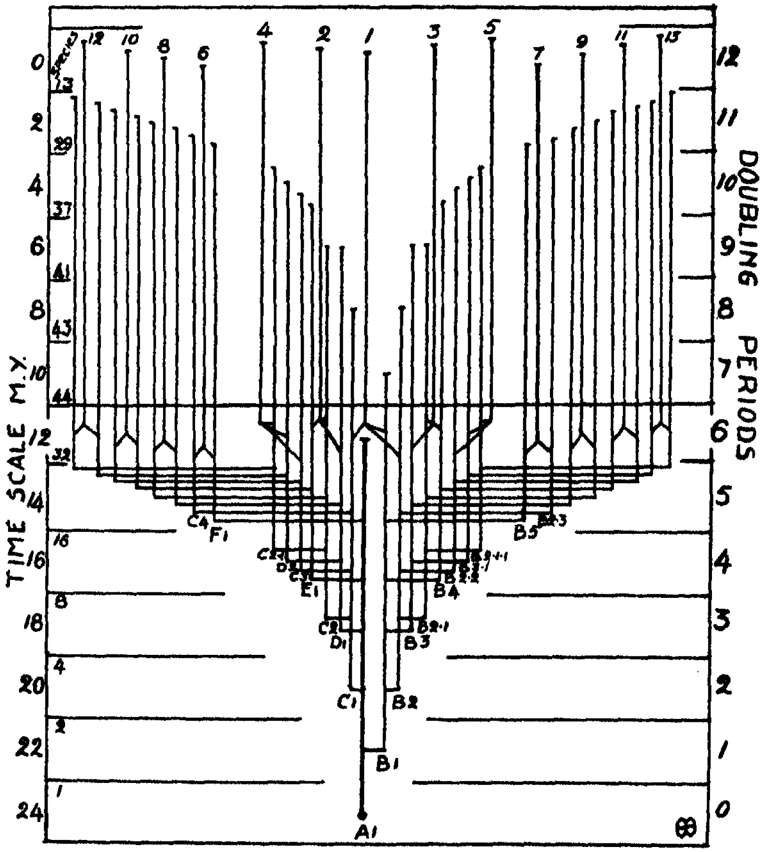


FIG. 2.—Diagrammatic history of the development and decay of an average genus of Angiospermæ.

This can be pictured in an informative fashion as in fig. 2, which is the result of many attempts to obtain a numerical arrangement which fits the data already observed and deduced, as well as other data which are developed later in connection with the Pliocene history of species-number, including the great majority of living species of flowering plants.

A genus is taken (fig. 2) as arising with one species A1. In the first doubling period this gives rise to a second species B1. In the second period each of these is taken as giving one more species C1 and B2. Yule's sN_τ progression with $s/g = 1{\cdot}5$ (Yule, 1924, p. 78) might have been used here, but we are considering free doubling and the difference is not sufficiently great to justify the complications, while with $s/g = 2{\cdot}1$ as for Compositæ the difference is considerably reduced. Yule himself (*op. cit.*, pp. 77–78) states that "When species are being killed-out, either more or less continuously during the whole lapse of time or more or less cataclysmically at intervals, it at once becomes doubtful how far equation (24) applies. I propose, therefore, to take it that, for present purposes, it suffices to assume the law of free increase as simply logarithmic from the beginning." Yule, throughout the last section of his memoir, favours the view of cataclysmic rather than continuous killing-out of species, so we may return to fig. 2 and proceed.

In the third period A1, B1, B2, and C1 each give a new species, making 4 origins and a total of 8 species. In the fourth period each of these 8 species throws a new one, giving 8 origins and a total of 16 species. In the fifth period each of these 16 species throws a new one, giving 16 origins and a total of 32 species. Then we come to the critical sixth period during which senescence develops; the first species A1 dies a normal death from old age, but senescence of the generic organisation also appears in this same period. Just as the species A1 shows senescent sterility in the production of fewer viable seeds to give fewer individuals, so the genus shows senescent sterility in the production of fewer new species.

Numerically it was found that 13 was the number at this point which gave satisfactory results in Table II. In the diagram this can be traced as follows: the species A1 is senescent and does not throw; B1, B2, and C1 are early derivative species approaching senescence and amongst the three there is only one chance of a new species (No. 1); then above and below the central older group we have derivative species, which are progressively farther away from their own period of senescent sterility in individuals but which are also progressively farther away from the central source, which is itself approaching senescence. Therefore we take each group of three species as giving a new one: 2, 3, 4, 5. Then from pairs of the relatively younger species which arose in the fifth period we derive 6, 8, 10, 12, 7, 9, 11, 13. But, with decay in species production or senescence in the genus, we normally derive no more new species. There occurs at this point a preparation of a "cataclysmic" extinction of the genus which *happens* after the lapse of 12 m.y.

In the sixth period, from 32 species, 13 new species arise and one old species dies, giving a total of 44 species. The genus then enters upon its mature phase, with species dying away slowly in the order in which they arose. In the seventh period only one B1 dies, giving a total of 43; in the eighth period 2 die, B2 and C1, giving a total of 41; in the ninth period 4 die, giving a total of 37; in the tenth period 8 die, giving a total of 29. Then the genus may be said to enter upon its final phase; in the eleventh period 16 die, giving a total of 13; the last 13 to arise survive to the twelfth period, and then, with their deaths, the genus normally comes to an end. This abrupt end appears to be the cataclysm which Yule suspected so strongly.

There is some evidence that there are a few genera which either have continued species production along a modification of the normal progression or have undergone a rejuvenation with a relatively sudden extensive diversification leading to the production of new sub-tribes or other groups of related genera. These few cases, however, stand out as exceptions, like the three large genera in Compositæ, which required special treatment (Small and Johnston, 1937) and are the subject of further special studies.

There is, of course, no suggestion that all genera conform to this average pattern. There are genera with more than 50 species to the extent of about 5 per cent. of the total genera in Compositæ (4·8 per cent.) and in Gramineæ (5·6 per cent.), although in the Birds this group is only about 1 per cent. (·98). These larger genera compensate to some extent for the smaller genera, which may never reach the size of 44 species, so that the average picture as given may actually be attained by less than 50 per cent. of genera. At any one stage in the upward phase of a group there will naturally be many more smaller genera than larger genera, but the comparison of frequency distributions in various groups has sufficient significance for a separate study.

The numerical totals for species-number throughout the life of an average genus would vary thus: 1, 2, 4, 8, 16, 32, 44, 43, 41, 37, 29, 13, 0 (fig. 2). This gradual rise to a peak, followed by a period of apparent stability, passing to a rapid decline, and ending in an abrupt disappearance, is generally recognised in the fossil record as the more or less typical history of many groups of extinct plants and animals. Here we find it appearing for a genus as a logical consequence of deductions made from the variation in Dp-ages of Compositæ, which is a relatively recent group and still the largest family of the Angiosperms. The pattern seems to be the same for a group of species as for a group of genera, but we may expect in related forms to find groups of genera showing longer life-times than groups of species, just as the life-time of a genus is at least twice that of a species.

The normal limitation of the maximum number of species in an ordinary genus to 44, as in the above series, would be at least a partial explanation of the excess of calculated over observed frequencies in the classes of genera with more than 40 species, which was noted in the original tests for Compositæ. The Grasses show a frequency distribution of generic sizes which does not differ significantly from Compositæ. The number of genera actually found in Compositæ with more than 50 species (37 out of 768) (Small and Johnston, 1937, Table III) is a clear indication that, while the series given may be normal for ordinary genera, there are some possibly ordinary genera which progress at least to the 64 stage before becoming senescent, and there are probably some few possibly primordial genera which progress still farther. What happens in 5 per cent. of genera need not prevent or distort a general view of what appears to be typical of the other 95 per cent. of the genera. In much the same way, there are a few groups of genera which show signs of decay in the production of new genera, so that normal death of species and decay in species-production within the genus is logically followed by decay in genera-production within the group or family. This senescence in the group or family is characterised by an M value about 5 to 15 and a very low $f1$ value or no monotypes at all. It can be traced in the Araucarieæ of the Coniferales, the Bambuseæ of the Grasses, and the Colymbidæ of the Birds. The percentage of genera involved is even lower than 5 in the groups so far investigated, but other, older groups may show this phenomenon dominating the normal type of distribution for generic sizes.

VIII. RESIDUAL DOUBLING IN SPECIES-NUMBER.

It is now possible to attempt to follow the residual doubling in species-number which is shown by groups of related genera, following the 1/K curve. Tabulating the totals, origins, deaths, and survivals for a group of genera, we can follow up with other genera arising in equal numbers in successive periods, rising to maturity and falling to decay along the same series. In this way we find the total number of species in any given period the same, also the total number and therefore the percentage of deaths constant for the various periods. This corresponds to the rectilinear extinction which is discussed above in Sect. IV. But it has been demonstrated that there is an average residual doubling of species-number with a doubling period of about six times the length of the free doubling period for species.

The relation between apparent Dp-ages and this residual doubling period is complex. Simple calculation would give six 12 m.y. periods at 72 m.y., five 12 m.y. periods at 60 m.y. where apparent Dp-age is observed as above 5·46 at 49 m.y.; four 12 m.y. periods at 48 m.y. compared again with the observed 5·46 at 49 m.y. Clearly the calculated apparent Dp-ages (with their corresponding M values) have a more complex relation to time than do ages in residual doubling periods as calculated in this simple manner. Nevertheless, the simplification of a uniform average doubling period enables us to continue the numerical analysis of the history of a group of related genera.

TABLE II.—SPECIES-NUMBER HISTORIES WITH DOUBLING OF GENERA AFTER 8 M.Y.

M.Y.	0	2	4	6	8	10	12	14	16	18	20	22	24	TIME
							45	32	16	8	4	2	1	TOTALS
							13	16	8	4	2	1	1	ORIGINS
	13	16	8	4	2	1	1							DEATHS
	0	13	29	37	41	43	44	32	16	8	4	2	1	SURVIVALS
	13	29	37	41	43	44	32	16	8	4	2	1		
	29	37	41	43	44	32	16	8	4	2	1			
	37	41	43	44	32	16	8	4	2	1				
	41	43	44	32	16	8	4	2	1					
	86	88	64	32	16	8	4	2	0					
	88	64	32	16	8	4	2	0						
	64	32	16	8	4	2	0	13						
	32	16	8	4	2	0	13	29						
	32	16	8	4	0·	13	29	37						
	16	8	4	0	13	29	37	41						
	8	4	0	13	29	37	41	43						
	4	0	13	29	37	41	43	44						
	0	13	29	37	41	43	44	32	16	8	4	2	1	
	450	391 +59	339 +52	303 +36	285 +18	277 +8	273 +4							
	244	140	68	32	14	6	2	LIVING						
	0	13	42	79	120	163	207	DEAD						
	100	59	28	13	6	2	1	L. ON BASE 100						
	0	3	10	19	29	39	50	D. ON BASE 50						
%S.	100	95	74	40	17	5	2	= % L./L.+D.						

In order to obtain the residual doubling, we must take into account the natural increase in genera which, with *s*/*g* above 1·0, would have a longer doubling period than that for species. If, therefore, we double the number of genera after every fourth species doubling period, the tabulation in Table II is obtained. This scheme gives the total species-number rising approximately along an exponential curve by 4, 8, 18, 33, 52, 59, from 273 to 450. The doubling is not complete in six periods.

The old genera dying-out within the period of time under consideration might be halved to correspond with the doubling of the new genera, and this would decrease the totals in the 12 m.y. column so much (from 273 to about 170) that doubling would be completed in about 8 m.y. instead of 12 m.y., since the total for the 8 m.y. column would then be 225, as compared with the 450 in the 0 m.y. column. The old genera would, however, belong to an older alliance somewhat different from the new one which is taken as developing, and the figures for the dead genera could be adjusted on less than a halving scale to give just complete doubling of total species-number in 12 m.y. The reduction of the "dead" numbers should, however, follow some biological principle, rather than a merely arithmetical adjustment, and it has not yet been found possible to give such an adjustment with a biological basis. In any case, 12 m.y. as the residual doubling period is only an average value, not an accurate one, for each period.

The numbers given throughout Table II are to be regarded more as proportions than as actual numbers of species, and they are useful in giving a rough idea of how the proportions of living and extinct species of a flora at any particular time might be arranged. The existing species decrease backwards along an exponential curve, while the extinct species form an increasing proportion of the flora; this increase is almost rectilinear with time, as after the first step the rise is about 40 for each 2 m.y. (Table II, fourth line up from base).

If the number of genera is doubled after every third species doubling period, we obtain a similar set of values, where in only five species doubling periods the total species-number rises by 14, 20, 40, 64, 83, 121, from 273 to 615, so that the doubling is completed within four periods (from 307 to 615). This rate of doubling is rather rapid, while that in Table II is rather slow. The appropriate doubling period for genera would seem to lie either between 6 and 8 m.y. with a 2 m.y. period, or about 8 m.y. with an adjustment of the "deads."

GENERIC DOUBLING PERIOD.—Taking 7 m.y. as the doubling period for genera in Compositæ, and starting with one genus at 70 m.y., the number of genera would increase thus: 2 at 63 m.y.; 4 at 56 m.y.; 8 at 49 m.y.; 16 at 42 m.y.; 32 at 35 m.y.; 64 at 28 m.y.; 128 at 21 m.y.; 256 at 14 m.y.; 512 at 7 m.y.; 1024 at 0 m.y. Actually there are nearly 800 existing genera of Compositæ, so that the 7 m.y. 2^n progression gives finally a reasonable approximation to the actual facts for number of living genera. A 2^n progression from 72 m.y. with an 8 m.y. period would give only 512 as a total, so that something more than an 8 m.y. speed and something less than a 7 m.y. rate of doubling is indicated.

If we try to follow this increase in generic-number in known genera, from the genera named in the original family tree (Small, 1919; Small and Johnston, 1937, fig. 1) there is *Senecio* at 70 m.y.; followed by *Gnaphalium* giving 2 genera about 63 m.y.; followed by *Spilanthes* and *Coreopsis* giving 4 genera about 56 m.y.; followed by *Bidens* and *Solidago* giving at least 6 (instead of 8, 2 of which may have become extinct) genera about 49 m.y.; followed by *Aster*, *Chrysanthemum*, *Achillea*, *Matricaria*, *Lactuca*, and *Trixis* giving at least 12 (as compared with 16) genera about 35 m.y.; followed by *Mutisia*, *Onoseris*, *Chaptalia*, *Siegesbeckia*, *Inula*, *Pulicaria*, *Gymnarrhena*, and *Erigeron* giving at least 20 (as compared with 32) genera about 28 m.y.; followed by the comparatively recent large extension up to all the existing genera. It is not suggested here that all these actual genera are to be considered as surviving for the whole of the geological period concerned, but the general approximation in actual generic numbers and the roughly geometrical increase shown is in reasonable agreement with a 7 m.y. 2^n progression of generic-number, especially when account is taken of the genera which have probably died out and of the genera which might have been named on the original tree.

Another detail upon which the scheme in Table II may be checked is the average number of species per genus in the last period (0 m.y.). At this stage there are 28 average genera with 450 species, giving an average number of species per genus (M) as 16, while for Compositæ as a whole the M value is 13·6 (Small and Johnston, 1937, p. 32), and 12·8 for Angiosperms taking 160,000 species and 12,517 genera (Willis, 1922, p. 180). Considering the very diagrammatic basis of Table II, this is a reasonable approximation, which would not be attained by an arrangement which did not include generic doubling, as this gives 12 genera with 270 species and an M value of 22·5.

IX. PLIOCENE BACKWARD EXTINCTION.

Using Table II and other similar tables as sources of data, we can calculate the apparent backward extinction which results from the progressive origin of new species combined with the actual extinction of old species. When dealing with now existing species, as distinct from total species-number, we can take only those in genera which began in or later than the period 12 m.y., because according to previous deductions no species which arose in 14 m.y. should be alive now. Therefore we consider only those figures within the outlined block. Describing these species as living (L) and the old extinct species as dead (D), we obtain from the lower half of Table II:

L 244–140–68–32– 14– 6– 2.
D 0– 13–42–79–120–163–207.

This gives, not the actual numbers of species, but the proportions of species L and D separately in each period; now the total species-number is found on other data to vary in such a way that on a percentage basis there would be 100 now and 50 at 12 m.y. Therefore we must convert the L series to base 100 and the D series to base 50; this gives approximately:

L 100–59–28–13– 6– 2– 1,
D 0– 3–10–19–29–39–50,

and then per cent. $\frac{\mathrm{L}}{\mathrm{L+D}}$ = 100–95–74–40–17–5–2.

Similar calculations using a table with a 6 m.y. doubling period for the genera give:

L 368–200–96–44– 20– 8– 2,
D 0– 13–42–79–120–163–207,

which gives approximately, on a 100 base and 50 base:

L 100–54–26–12– 5– 2–·5,
D 0– 3–10–19–29–39–50,

and then per cent. $\frac{\mathrm{L}}{\mathrm{L+D}}$ = 100–95–72–39–15–5–1.

The difference in the rate of generic doubling (8 m.y. in Table II and 6 m.y. in the other table used) makes practically no difference to the series of apparent backward extinction percentages, or percentage survivals.

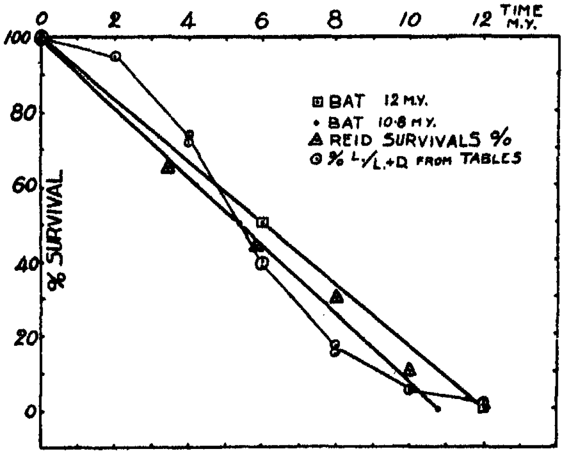


FIG. 3.—Percentage survivals and extinctions for Pliocene.

We can now graph these percentages as survivals for comparison with rectilinear backward extinctions as derived from the BAT curve, using both 10·8 m.y. and 12 m.y. for sub-total extinction; and also mark the points for the Reid percentage extinctions which, when converted to survival percentages, are on a strictly comparable basis. These are all given in fig. 3, where it will be seen that the percentage survivals derived from Table II vary more or less symmetrically around the BAT straight line, while the Reid points all lie on or near the straight line also.

The numerical analysis of generic history given in Table II is clearly only an approximation, but with some degree of verisimilitude when compared with the points given by Reid and the points derived from the BAT curve. The numerical arrangement requires smoothing, and this may be accomplished by a mathematical treatment of this and other parts of the subject, as is indicated by further investigations. As yet we can obtain rectilinear extinction as for the BAT curve with no residual increase in species-number, and also an approximation to exponential increase to final doubling but with a sigmoid extinction line. The full solution might include a less steeply exponential increase, and might involve reductions in the total "deads" in accordance with the generic increase assumed during the last 12 m.y. Another possible variation is the use of a less abrupt ending for the genus. All these and many other modifications have already been investigated, but the solution given in Table II remains the one which is the best compromise between the requirements for doubling in total species-number in 12 m.y. and those for a rectilinear extinction.

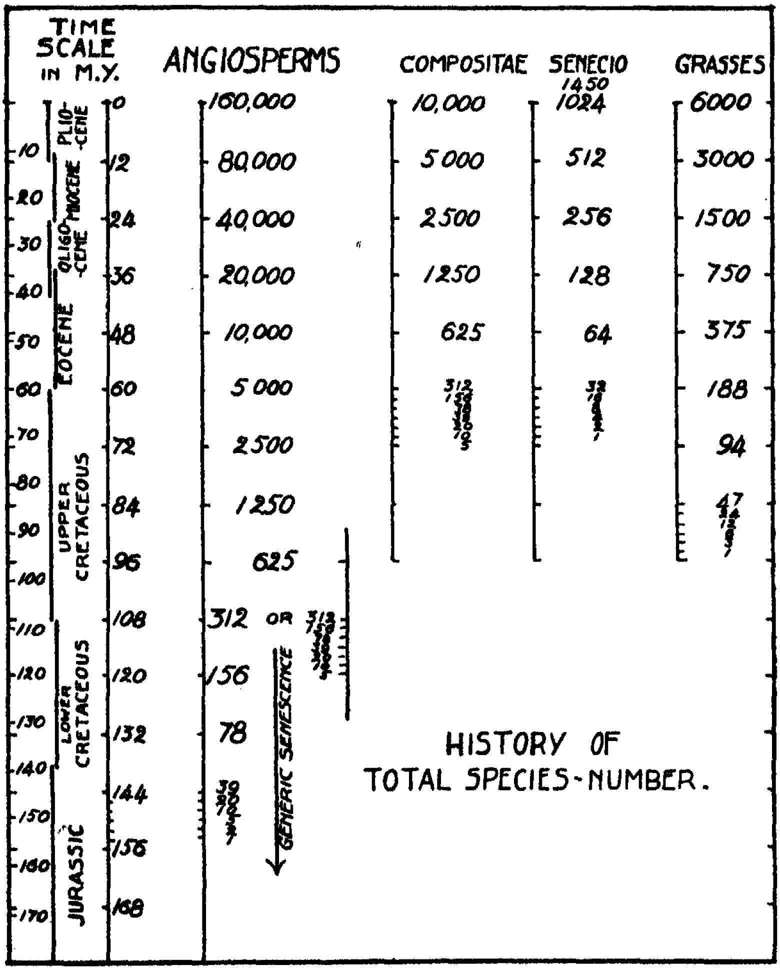
X. GEOLOGICAL HISTORY OF SPECIES-NUMBER.

Distinguishing carefully between existing species which have arisen on a 2 m.y. progression and species-number which has increased along a 12 m.y. progression, we can now attempt to trace the approximate course of species-number increase during geological time.

COMPOSITÆ.—On the above basis we can trace the history of species-number in Compositæ backwards through the Cenozoic. Taking 10,000 as the present number and halving for each 12 m.y., we reach 312 species at the base of the Eocene (60 m.y.). The Compositæ are considered on other grounds as having arisen in Late Upper Cretaceous, so that at this point we take note of the consideration that, with 12 m.y. and 2 m.y. progressions, there will be no deaths for the first 11 or 12 m.y. from the origin. This leads to a halving of species-number every 2 m.y. backwards from 60 m.y., giving only 5 species at 72 m.y., which is in reasonable accordance with the general view of the family as previously presented (Small, 1919).

ANGIOSPERMS.—The Compositæ, as a relatively young family, should not show much sign of the senescence of whole groups of genera, but the Angiosperms, as a much older group, probably have their history complicated by the senescence of genera and of whole groups of genera. By repeated halving of the 160,000 for existing species of Angiosperms we reach 312 at 108 m.y., but continue with the 12 m.y. period to 39 at 144 m.y., and then by 2 m.y. stages to 1 at 154 m.y. Even this may be too late a date for the origin of the Angiosperms, and a large degree of generic senescence would push the origin at least lower down in the Jurassic.

TABLE III.



The sudden rise of the total species-number to 312 at the end of Lower Cretaceous and to 5000 by the end of the Upper Cretaceous may account for the palæontologists' (Schuchert and Dunbar, 1933, p. 367), "Deciduous trees suddenly became conspicuous in the Early Cretaceous and long before the close of the period dominated the landscape in all continents just as they do to-day." "The strong deployment of this group of plants in the

Cretaceous was one of the most significant advances in the whole evolution of plant life, second only to their spread over the lands."

SENECIO.—This genus appears to be exceptional among Angiosperms. While Compositæ species form rather more than 6 per cent. of the total existing Angiosperms, *Senecio* alone has about 10 per cent. of the species of Compositæ, so that this single genus has over 0·6 per cent. of the total species-number in Angiosperms. These species, it should be noted, extend into all parts of the world and are recognised Linnean species, not segregates such as occur in *Hieracium* and other so-called critical genera. *Senecio* thus appears not only as now a primitive genus, but also as the basal and central continuous stock from which other Compositæ have been derived, directly or indirectly. The history of species-number in *Senecio* is, therefore, worth following. Starting with one species at 70 m.y., doubling for each 2 m.y. through the first five doubling periods, and then for each 12 m.y. from 60 m.y. to the present, we get a total of 1024 species, as compared with the 1450 mentioned for *Senecio* by Willis (1922, p. 185). A very slight allowance for post-Pliocene time would give even closer approximation of the calculated and observed sizes for this genus. It is, therefore, quite possible on the basis of species-number that *Senecio* as a genus has existed throughout the entire period of existence of the Compositæ. The species-number history may involve at least two periods of senescence and rejuvenescence in this genus, but rejuvenescence is the subject of later studies. Other genera are, of course, known from Cretaceous times such as *Platanus*, *Cinnamomum*, *Quercus*, *Juglans*, *Salix*, *Ficus*, etc. (Seward, 1933, p. 404).

GRASSES.—In a previous contribution (Small, 1937, Q.E. III, fig. 1) the species-number of the Grasses was given to show that this type of data conformed to the suggested geological history of the family. Starting with the existing 6000 as a species-number and halving at 12 m.y. intervals, we reach 47 at 84 m.y., and 1 at 94 m.y., giving an Upper Cretaceous origin for the Gramineæ, which is considerably lower than that for Compositæ. The 12 m.y. series is extended beyond the 188 at 60 m.y. because the Dp-age for the Bambuseæ, as the basal group, is considerably lower (4·65) than that of the Paniceæ (6·33), which is very probably a derivative group, thus indicating an extensive generic senescence which has affected the Gramineæ but not the Compositæ, where the basal and oldest group still shows the highest Dp-age. These divergences in groups known to be old are not fundamental flaws in the general quantitative treatment; rather are they significant exceptions to rules which obviously apply to a large proportion of species and genera, leaving the exceptions to furnish the clues for subsequent investigations.

XI. PRIMORDIAL GENERA.

The ordinary generic history outlined above involves a distinction between ordinary genera, which do not develop more than about 44 to 64 species, and those *primordial* genera which occur in many families, as the basal genera of sub-tribes, tribes, or whole families. *Senecio* is an outstanding example, but there are others even in Compositæ, such as the *Eupatorium-Mikania* group for the Eupatorieæ and the *Centaurea* plexus for the Cynareæ. The 26 out of 768 genera in Compositæ with 66 or more species may all be considered as possible primordial genera. This again opens up a special field for investigation throughout the flowering plants, because many tribes and families do not appear to have primordial genera, while others have; and these phenomena can also be traced in animal genera and groups of genera.

XII. THE PRESENT RATES FOR ORIGINS AND EXTINCTIONS.

Confining the calculations to Angiosperms, it is now relatively easy to estimate the present rates for origin of new species and extinction of old species.

ORIGINS.—With a doubling period of 2 m.y. and a present total of about 160,000 species of Angiosperms, there are 160,000 new species due to arise in the next two million years. Since this increase should really be exponential within itself, we err on the larger side by taking the average at 16 in 200 years, or 8 per century. The chances of all 8 origins being witnessed, or detected with certainty, are very small, but at least one, namely, that of *Capsella Hœggeri*, is known to have taken place under circumstances which involved its immediate recognition. Other less certain cases make a total of more than 8 during the last century.

EXTINCTIONS.—With existing species arising along a 2^n progression with a 2 m.y. period, we get 80,000 at 2 m.y.; 40,000 at 4 m.y.; 20,000 at 6 m.y.; 10,000 at 8 m.y.; 5000 at 10 m.y.; 2500 at 12 m.y.; and 1250 at 14 m.y. It is suggested above that at least 99 per cent. of existing species did not exist more than 12 m.y. ago, and this agrees with 1250 species at 14 m.y. There should be, therefore, 1250 to 2500 species in a senescent condition at the present time, these having arisen about 12 m.y. ago. Since these would include known sterile or semi-sterile species and relic endemics, and since the maximum of 2500 species are due for extinction in the next half-million years, the present rate of natural extinction may be as low as five in one thousand years. This natural rate is definitely lower than the observed rate of extinctions, but many of these extinctions are traceable to the unnatural treatment of rare species by collectors, and some of these rare and now extinct species were very possibly new species, discovered and "collected" to extinction before they had time to spread.

SUMMARY AND GENERAL CONCLUSIONS.

I. Further points are determined along the BAT curve, especially for the last twelve million years (Table I).

II. The year value of the Dp-age unit is checked, by reference to these values and to the suggested length of the Pleistocene, and is found to be 2·0 or 2·08 m.y.

III. The reciprocals of the K values are given, and their significance, in relation to the conclusions from the rectilinear increase of K values with time, is discussed. They are interpreted as indicating (1) rectilinear backward extinction, giving 50 per cent. extinction at 5·4 m.y. and sub-total extinction at 10·8 to 12 m.y.; and (2) a residual increase in species-number with an average doubling period of 12 m.y. This gives 10·8 to 12 m.y. as the *average* life-time for a species (fig. 1).

IV. Sub-total extinction, with a rectilinear relation to time, when percentage extinction is calculated as percentage of existing species over existing and extinct species at the various points of time, is compared with the hollow curve of backward extinction along a 2 m.y. progression for the percentage of living species calculated as the percentage of now living species existing at the various points of time over the total of species now living. A comparison, showing a close similarity, is also made of the rectilinear backward extinction with Mrs Reid's data for a Pliocene flora, which gives about 12 m.y. as the *maximum* life-time for a species.

V. The basis of the interpretation of 1/K values as a measure of the increase in species-number is explained. It is then emphasised that these various conclusions lead to the same or similar values for both the average life-time and the maximum life-time for a species.

VI. From this the important deduction can be made that species die a normal death, presumably from the senescent sterility of old age, with, perhaps, a minor part being played by the progressive restriction of survival conditions for a senescent species.

VII. The life-history of a genus is explained upon the foundation of the above conclusions, and species-number in a genus is shown to follow the series 1–2–4–8–16–32–44–43–41–37–29–13–0. This gives 24 m.y. as the normal life-time of an ordinary genus, and a diagram is given showing the effects of species-deaths at 12 m.y. and the decay of species-production within a genus also at the 12 m.y. period. The significance of this picture of generic history is considered in some detail (fig. 2).

VIII. A numerical analysis is made of a group of genera, and the residual increase in species-number with a 12 m.y. doubling period is shown as following an increase in the number of genera within the group; this increase appears to have a doubling period of a length between 7 and 8 m.y. (Table II). A doubling period of 7 m.y. is shown to agree with generic-number in Compositæ at various geological periods.

IX. The percentage of backward extinction in the above group of genera is traced from Table II, as a sigmoid curve, varying symmetrically around the rectilinear backward extinction line derived from three sources, namely, the BAT curve data (Table I), Reid's Pliocene extinction data (see Table I), and the generic history scheme in Table II (see fig. 3).

X. The geological history of species-number is traced for Compositæ, Angiosperms, *Senecio*, and the Grasses, and is shown to be in reasonable agreement with data derived from other sources (Table III).

XI. A distinction is drawn between ordinary genera, which form the large majority, and primordial genera, which develop more than 65 species and are relatively few in number.

XII. The present rate for origins of new species in Angiosperms is shown to be about eight per century, while the present rate for the natural extinctions is estimated to be about five in one thousand years.

GENERAL CONCLUSIONS.—The close approximation of the various quantitative considerations, derived from Yule's formulæ and the BAT curve, to the various data which are available from other sources forms a cumulative series of possible coincidences, the sum-total of which gives an increasing verisimilitude to the whole subject of quantitative evolution. The other sources include general species-number in Angiosperms, Grasses, Compositæ, and *Senecio*, general generic-number in the Compositæ, together with Reid's Pliocene extinction data as above; the general evolutionary sequence for Compositæ (Small, 1919) and for the Grasses (Bews, 1929); also Udny Yule's tests for Cerambycinæ, Chrysomelidæ, Snakes, Lizards, and Leguminosæ (Yule, 1924). Other, still unpublished, investigations indicate that while the Oligochæte worms follow the general scheme, the Coniferæ show a 5 m.y. and 30 m.y. curve; also that the non-Passerine birds show distinctly modified data which can be interpreted as showing the effects of competition between related species to an extent of at least 60 per cent. in the genera of that group, while the Passeres show the effects of this type of natural selection to the extent of not more than 42 per cent. in the genera in that large group of birds.

With this basis of evidence as a background, a definite conclusion may still be premature, but we are certainly justified in suggesting as tentative conclusions (1) that the laws of chance have acted as a basal scheme in the mutational origin of new species, more or less along the lines elucidated by Udny Yule (1924), with the important modifications of normal death of species after a limited life-time and of normal decay in species-production within ordinary genera; (2) that competition between species has played a very minor part (possibly 1 per cent.) in the diversification and survival of species and genera in Angiosperms, although it can be shown to have had a distinctly measurable effect upon the history of species and genera in some groups of animals.

If the data given in these contributions to the quantitative study of evolution appear, in the phraseology of one critic, to be too coherent for actual truth, it should be remembered that, so far as we have gone, these investigations have covered only the ground plan or basic framework of the evolution of species and genera, mainly in Angiosperms; and that it is at least possible such a framework does exist. The variations upon the fundamental theme appear to be many, and their very multiplicity may well be responsible for the appearance of incoherence which seems to be the most desirable feature of a really popular view of evolution in general.

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V.—The Decline of the Birth-Rate: Regularities Revealed by an Analysis of the Rates Observed in Certain European Countries.

By **R. S. Barclay,** B.Sc., and **W. O. Kermack,** D.Sc., LL.D. (From the Laboratory of the Royal College of Physicians, Edinburgh.) (With Two Figures and Fourteen Tables.)

(MS. received December 1, 1937. Read December 6, 1937.)

INTRODUCTORY.

DURING recent decades the vital statistics of the more developed countries of the world have exhibited two outstanding features: the first is a decline in the death-rate, and the second a similar decline in the birth-rate, the latter setting in some time after the former. It is generally realised that, for an adequate study of the changes involved, it is necessary, not merely to consider the crude death- and birth-rates—that is, the number of deaths and births respectively per 1000 inhabitants—but also to take into account the age distribution of the population. In the case of death-rates, for instance, it is important to know the specific death-rates for each age-group—that is to say, for example, the annual number of deaths of persons aged twenty, per 1000 individuals of that particular age. In the same way the crude birth-rate can only be properly interpreted when analysed in reference to the age of the mothers.

For most countries which collect vital statistics the specific death-rates are easily obtainable, for the age at death is almost invariably recorded on the death certificate. These rates are tabulated in the respective Registrar-General's reports: for Scotland as from 1860, and for England and Wales as from 1841. During the past half-century they show a more or less steady decline, which, however, does not seem to follow any simple law. In two recent papers (Kermack, McKendrick, and McKinlay, 1934 and 1935) it has been shown that, in spite of the apparently arbitrary nature of the decline, there is an underlying regularity of a simple and interesting type. To bring out this regularity, it is only necessary to choose as standard the specific death-rates which prevailed before the decline had begun, and to represent the specific death-rates for subsequent periods as percentages of the corresponding standard rates. If the figures so obtained are collected in a table, such as that shown in Table I (for

Scotland; reproduced by kind permission of *The Lancet*), it will be seen that, apart from small fluctuations of a more or less accidental character, they exhibit an unexpected and interesting regularity—along each diagonal the figure is approximately constant. The implications of this result are discussed at some length in the two papers referred to above. It is sufficient here to point out that it follows that the actual specific death-rate recorded for any age-group is the product of two factors, one depending on the year of birth, the other on the actual age of the group in question. This generalisation allows certain predictions to be made with regard to future death-rates. It should be added that the result holds for all groups from the age of five years and upwards; the infantile death-rate follows a different course.

TABLE I.—RELATIVE SPECIFIC MORTALITY RATES, SCOTLAND.

AGE / YEAR	1860	1870	1880	1890	1900	1910	1920	1930	
0	100	104.5	97.5	104	102	88	75	64.5	
10	100	108	85	69	55	45	36.5	30.	
20	100	104.5	87	76.5	63.5	47.5	42	34.5	
30	100	109	91	86	79	56	50	39.5	40
40	100	111	98.5	100.5	91	69	59	51	50
50	100	114	108	115.5	110.5	88.5	73	66	60
60	100	110	110	126.5	125.5	103.5	91	81	80
70	100	97	96	110.5	108.5	97.5	90.5	88.5	
OVER 75	100	96.5	88.5	98	94	88	90	91	90

An exactly similar regularity is found in the figures for England and Wales, and in the case of Sweden, where specific death-rate figures are available from 1751 onwards, the same general regularity is to be observed; only here it is somewhat obscured by a disturbance, which, since 1855, has affected the age-groups centred at 10, 20, and 30 years.

In the light of these results it is natural to inquire whether the decline in the fertility of mothers exhibits any similar regularity. It is necessary first of all to construct a table showing the specific fertility rates for mothers of various ages in successive calendar years. For this investigation the records must extend backwards to a time preceding the beginning of the modern decline in the birth-rate. This very much limits the countries which can be dealt with, for there are very few governments which have for any length of time insisted on the statement of the mother's age on the birth certificate. It is only now being realised how grave a blow was struck at the progress of knowledge in this field when the recording of this information was discarded in Scotland in 1855, after having been carried out for but one year. Most civilised countries have already taken the necessary steps to ensure the recording of the mother's age on the birth certificate. The decision recently taken to adopt this practice in Great Britain, though belated, is nevertheless a most welcome one.

DEFINITIONS.

Before proceeding to draw up fertility tables for the various countries, it is necessary to decide which of two alternative indices of fertility is to be adopted. We may either consider the total number of children born to mothers of a particular age per 1000 women of that particular age (*specific total fertility rates*); or deal with only legitimate births, and find the number of children legitimately born to married women of a particular age per 1000 married women of that particular age (*specific legitimate fertility rates*). From the biological point of view, importance attaches to the specific total rates; but when the interpretation of the figures in terms of known social factors is the objective, the legitimate fertility rates are especially useful, because they refer to more homogeneous groups. As will be seen later, approximately the same results are obtained whichever set of figures is employed.

SPECIFIC LEGITIMATE FERTILITY RATES IN SWEDEN, DENMARK, AND FINLAND.

In Sweden the necessary data are available from 1781 onwards. Table II gives the quinquennial legitimate fertility rates for this country as supplied by the Central Bureau of Statistics, Stockholm (cf. *Statistisk Årsbok för Sverige, 1931*). It will be seen that the rates for the four decennial periods 1841–50, 1851–60, 1861–70, and 1871–80 are all approximately the same; the fall in the birth-rate only began about 1880. We have therefore taken as standard the average of the rates for the four

TABLE II.—SPECIFIC LEGITIMATE FERTILITY RATES, SWEDEN, 1841–1934.

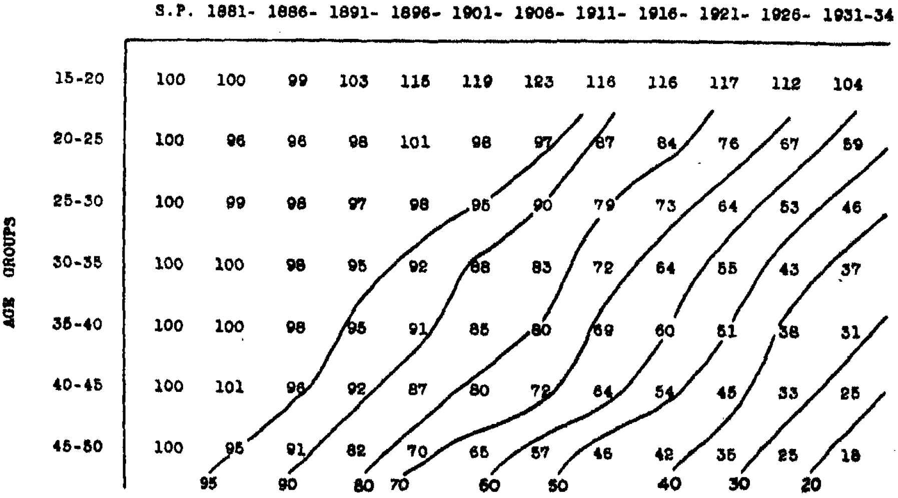
Age-groups.	Standard Period.	1841–50.	1851–60.	1861–70.	1871–80.	1881–85.	1886–90.	1891–95.
15–20	512·9	502·6	520·1	506·2	522·6	510·2	506·6	529·3
20–25	464·6	456·7	470·4	457·2	474·1	447	447	456
25–30	378·3	370·0	378·0	376·0	389·2	376	372	365
30–35	324·2	316·8	326·8	320·4	332·7	325	318	307
35–40	257·0	245·2	258·2	258·4	266·3	258	253	243
40–45	148·0	136·3	148·1	152·3	155·4	150	142	136
45–50	24·3	23·1	24·5	24·8	24·6	23	22	20

Age-groups.	1896–1900.	1901–05.	1906–10.	1911–15.	1916–20.	1921–25.	1926–30.	1931–34.
15–20	589·4	609·4	629·1	594·3	596·3	601·7	575·2	534·6
20–25	467	456·1	449·8	403·8	392·3	354·5	309·1	273·6
25–30	369	358·9	341·0	298·6	276·8	242·4	198·7	174·4
30–35	297	286·1	269·7	231·8	208·9	178·3	139·9	121·0
35–40	234	218·3	204·8	178·3	154·1	129·9	98·2	78·3
40–45	129	118·1	107·1	94·3	80·4	66·0	48·3	36·2
45–50	17	15·7	13·8	11·2	10·2	8·5	6·0	4·3

These rates are based on confinements, not actual births.

The last calendar period extends over four years, as the necessary informatiön is not available for 1935.

TABLE III.—RELATIVE SPECIFIC LEGITIMATE FERTILITY RATES, SWEDEN.



AGE GROUPS	S.P.	1881-	1886-	1891-	1896-	1901-	1906-	1911-	1916-	1921-	1926-	1931-34
15-20	100	100	99	103	115	119	123	116	116	117	112	104
20-25	100	96	96	98	101	98	97	87	84	76	67	59
25-30	100	99	98	97	98	95	90	79	73	64	53	46
30-35	100	100	98	95	92	88	83	72	64	55	43	37
35-40	100	100	98	95	91	85	80	69	60	51	38	31
40-45	100	101	96	92	87	80	72	64	54	45	33	25
45-50	100	95	91	82	70	65	57	46	42	35	25	18

decennial periods. These *standard rates* are shown in the column headed *standard period.* When the other figures are divided, each by the corresponding standard rate, we obtain the *relative specific legitimate fertility rates* shown in Table III. For convenience, the actual quotients have been multiplied by 100 so as to give the results as percentages.

It will be seen that, if we except the 15–20 age-group, these figures exhibit a degree of regularity comparable with that shown by the relative specific death-rates as described above. Thus, for example, the line which passes through the groups possessing 60% of the standard fertility is nearly straight, and lies along a diagonal. Other parallel diagonals correspond approximately to 40%, 50%, 70%, etc.

Although, then, the decline in the Swedish birth-rate, when analysed, is found to contain certain regularities of the same general type as those met with in connection with the death-rates, there is, nevertheless, one very striking difference. The diagonals along which the relative figures are constant are the ones at right angles to those found in the case of the death-rates.

At this point it is desirable to inquire whether this result for Sweden stands by itself, or whether it holds for other countries for which adequate statistical data are available. In the case of Denmark, for example, information is obtainable for 1861 onwards. The data, as furnished by the Department of Statistics, Copenhagen, are presented in Table IV (cf. *Statistisk Tabelvaerk (Danmark), 1926–30*). Though the statistics do not begin at so early a date as in Sweden, they include periods before any appreciable decline in the birth-rate set in. The standard figures, calculated from the periods 1861–70 and 1871–80, are also given in the table.

When the other figures in the table are divided by the corresponding standard rates, and multiplied by 100, the *relative specific legitimate fertility rates* (Table V) are obtained. It is again evident that, apart from the age-group 16–20, there is the same diagonal regularity in the Danish figures as in the Swedish.

The only other country for which we have been able to obtain even moderately adequate figures is Finland. The specific legitimate fertility rates for this country are shown in Table VI, and the relative rates, calculated in the usual way, in Table VII. In this case the standard rates are derived from the periods 1880–84 and 1885–89. The general diagonal trend is obvious, though the figures are somewhat less regular. Inspection of the table reveals that disturbance is principally due to the European War, the period 1915–19 showing abnormally low rates, and the post-War periods abnormally high rates. There is, of course,

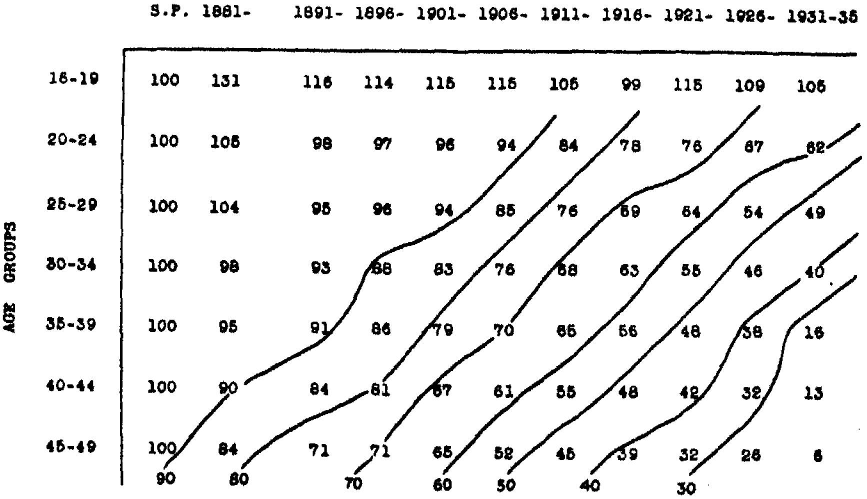
TABLE IV.—SPECIFIC LEGITIMATE FERTILITY RATES, DENMARK, 1861–1935.

Age-groups.	Standard Period.	1861–70.	1871–80.	1881–90.	1891–95.	1896–1900.	1901–05.
16–19	545·5	468	623	715	633	620	628
20–24	469·5	447	492	494	459	457	451
25–29	388·0	389	387	405	367	371	365
30–34	317·0	312	322	312	295	280	262
35–39	243·0	236	250	230	222	208	191
40–44	126·5	130	123	114	106	102	85
45–49	15·5	17	14	13	11	11	10

Age-groups.	1906–10.	1911–15.	1916–20.	1921–25.	1926–30.	1931–35.
16–19	626	574	542	629	595	574
20–24	441	393	368	359	314	293
25–29	328	295	269	250	210	189
30–34	240	214	199	175	146	127
35–39	171	157	135	117	93	40
40–44	77	69	61	53	40	16
45–49	8	7	6	5	4	1

These rates are based on numbers of births, not confinements.

TABLE V.—RELATIVE SPECIFIC LEGITIMATE FERTILITY RATES, DENMARK.



AGE GROUPS	S.P.	1881-	1891-	1896-	1901-	1906-	1911-	1916-	1921-	1926-	1931-35
16-19	100	131	116	114	115	115	105	99	115	109	105
20-24	100	105	98	97	96	94	84	78	76	67	62
25-29	100	104	95	96	94	85	76	69	64	54	49
30-34	100	98	93	88	83	76	68	63	55	46	40
35-39	100	95	91	86	79	70	65	56	48	38	16
40-44	100	90	84	81	67	61	55	48	42	32	13
45-49	100	84	71	71	65	52	45	39	32	26	6

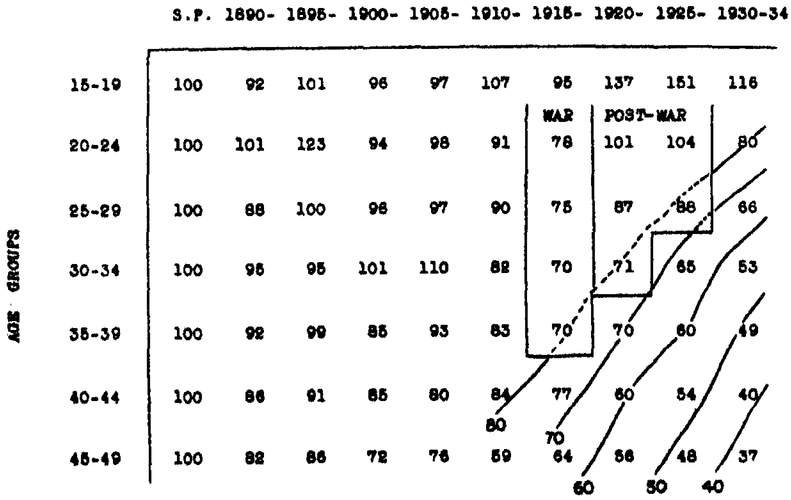
TABLE VI.—SPECIFIC LEGITIMATE FERTILITY RATES, FINLAND, 1880–1934.

Age-groups.	Standard Period.	1880–84.	1885–89.	1890–94.	1895–99.	1900–04.
15–19	386·2	383·9	388·5	353·4	388·6	369·0
20–24	430·3	423·0	437·5	436·0	528·5	405·5
25–29	371·0	359·2	382·8	327·3	369·9	354·8
30–34	338·0	333·7	342·2	319·4	322·7	342·9
35–39	270·3	265·0	275·5	248·2	268·3	230·9
40–44	175·7	169·6	181·8	151·7	160·3	150·1
45–49	29·6	26·7	32·4	24·2	25·4	21·4

Age-groups.	1905–09.	1910–14.	1915–19.	1920–24.	1925–29.	1930–34.
15–19	373·8	411·8	365·8	529·9	584·9	449·2
20–24	422·1	390·7	333·9	435·1	447·1	343·9
25–29	361·2	332·7	276·8	323·0	326·5	243·9
30–34	372·3	277·6	238·2	238·4	218·0	179·5
35–39	251·6	224·8	189·3	189·0	162·4	132·7
40–44	140·2	147·9	134·7	105·6	95·5	70·0
45–49	22·4	17·4	18·8	16·5	14·1	11·1

We understand these rates are based on numbers of confinements.

TABLE VII.—RELATIVE SPECIFIC LEGITIMATE FERTILITY RATES, FINLAND.


WAR
POST-WAR
80
70
60
50
40

AGE GROUPS	S.P.	1890-	1895-	1900-	1905-	1910-	1915-	1920-	1925-	1930-34
15-19	100	92	101	96	97	107	95	137	151	116
20-24	100	101	123	94	98	91	78	101	104	80
25-29	100	88	100	96	97	90	75	87	88	66
30-34	100	95	95	101	110	82	70	71	65	53
35-39	100	92	99	85	93	83	70	70	60	49
40-44	100	86	91	85	80	84	77	60	54	40
45-49	100	82	86	72	76	59	64	56	48	37

absolutely no doubt that major cataclysms, such as great wars or epidemics, produce well-marked temporary effects on both death-rates and birth-rates. However, as compared with the deeper social influences, such disturbances, though violent, are but temporary in their incidence. For our present purpose they are to be regarded only as perturbations superimposed on a more permanent secular trend.

We conclude that in Sweden and Denmark, and, apart from War disturbances, in Finland, the specific legitimate fertility rates follow what we may call the *diagonal law*. Women under twenty must be excluded in each case.

SPECIFIC TOTAL FERTILITY RATES IN SWEDEN AND DENMARK.

The specific total fertility rates may be analysed in exactly the same way. The necessary data for Sweden and Denmark are given by Kuczynski (1935). The relative rates, obtained by dividing these figures by the corresponding standard rates, are shown in Tables VIII and IX. In the case of Denmark the rates for the seven-yearly period 1878–84 are taken as standard; for Sweden the average over the first two quinquennial periods, 1871–75 and 1876–80, has been adopted. Once more the diagonal regularity is revealed; it is to be noted that the age-group 15–20 again stands out, in both cases, as an exception, and that, indeed, the next age-group, 20–25, is also irregular and deviates in the same sense.

NORWAY AND FRANCE.

For two other European countries we have been able to obtain records of specific fertility rates extending over a considerable period—Norway and France (*cf.* respectively *Folkemengdens Bevegelse, 1921–32*, and *Statistique du Mouvement de la Population, 1935*). In both cases, however, the figures are not particularly suitable for the present investigation, and so will not be discussed in detail in this paper. The Norwegian statistics are available only for ten-yearly periods, and so the above form of analysis cannot be directly applied. It may be stated, however, that there is a general qualitative agreement of the Norwegian with the Swedish and Danish figures, and, in particular, that the approximate diagonal law is clearly indicated. The French statistics go back to 1896, but here the difficulty arises that the decline in the French birth-rate had been proceeding during most of the nineteenth century, so that the direct calculation of a standard period is out of the question. However, by the application of the modified method developed in connection with the death-rates (Kermack, McKendrick, and McKinlay, 1935), this difficulty

TABLE VIII.—RELATIVE SPECIFIC TOTAL FERTILITY RATES, SWEDEN.

AGE GROUPS	S.P.	1881-	1886-	1891-	1896-	1901-	1906-	1911-	1916-	1921-	1926-30
15-19	100	108	113	121	154	166	198	204	177	187	186
20-24	100	99	101	101	109	112	115	107	99	91	78
25-29	100	97	95	93	93	93	89	78	71	63	51
30-34	100	96	94	89	87	83	79	68	60	52	41
35-39	100	96	93	88	85	78	73	64	54	46	35
40-44	100	95	90	86	81	73	66	58	49	40	29
45-49	100	91	89	78	68	62	54	44	39	33	23

90 80 70 60 50 40 30

TABLE IX.—RELATIVE SPECIFIC TOTAL FERTILITY RATES, DENMARK.

AGE GROUPS	S.P.	1885-94	1895-	1901-	1906-	1911-	1916-	1921-	1926-30
15-19	100	110	123	145	174	169	157	170	162
20-24	100	100	106	108	112	104	97	92	81
25-29	100	97	95	94	87	78	72	67	56
30-34	100	92	85	81	75	66	61	53	45
35-39	100	96	89	79	71	63	56	49	39
40-44	100	95	83	70	64	57	50	43	33
45-49	100	86	77	68	55	51	43	38	29

90 80 70 60 50 40 30

is avoided, and it then appears that the diagonal law held good up to the beginning of the War. The War, of course, brought about a general fall in the birth-rate, and this was followed by a rapid rise above the pre-War level. The rate soon returned to more normal values, but continued to remain higher than would have been the case if the pre-War diagonal law had still prevailed. We are not in a position to express an opinion as to how far administrative measures, such as the system of family allowances, has contributed to this effect.

DISCUSSION.

The most striking contrast between the death-rate and birth-rate figures consists in the fact that in the latter case the diagonal lines lie at right angles to those obtained in the former. This expresses the fact that whereas the death-rate first began to fall in the younger age-groups, the decline in the fertility of married women was initially limited to the older women, and only gradually spread to the younger age-groups. Qualitatively, this is perhaps not surprising; in general, the older women would, on the average, have the larger families, and it is natural that limitation should be first applied to the very large families, and only afterwards to the smaller ones. What is very surprising is that decrease in fertility should have followed so regular a course as to give the approximately linear relationship demonstrated by the tables. It is even more curious that the lines should run at 45°. This means that the wave of reduced fertility, sweeping down from the older to the younger women, passes from one quinquennial age-group to the next in precisely five years. In the case of the death-rates the wave of reduced mortality swept in the opposite direction, from the young to the old, and it was pointed out that here the existence of the diagonal law meant that each generation carried its own characteristic reduction in mortality along with it. In the case of the birth-rates there does not seem to be any corresponding simple interpretation. At present we can only regard the fact that the rate at which the wave progresses is one year of age per year of time as a curious accident.

Although the theoretical implications of these regularities in the decline of fertility are somewhat obscure, the linearity of the law makes its practical application easy, as in the case of the death-rates. Straight lines may be extrapolated without ambiguity, and so it is possible to extend the table for one or two periods. The limit to which this extension can be safely carried out is determined by three main factors. Firstly, the linearity is, doubtless, only approximate, and sooner or later a significant curving will occur, leading ultimately to a considerable divergence of the actual from the expected fertilities. Secondly, the farther we proceed into the future, the greater is the likelihood of violent disturbances and entirely new factors being encountered, which might introduce very great discrepancies. Thirdly, the percentage reductions for the higher age-groups are not directly given for future years. The number of these missing rates becomes progressively greater as time goes on. These older age-groups will not at first greatly affect the total birth-rates, as they are relatively infertile, and in any case an approximate estimate of the percentage required can be made by extrapolating from the known sequence of percentages; but prolonged extrapolation becomes increasingly uncertain, and the groups affected become more and more important.

In the table below (Table X) we give estimates of the specific legitimate fertility rates for Sweden for the next two quinquennial periods. It will be interesting to see how far these figures will be verified by the actual facts.

TABLE X.—CALCULATED FUTURE SPECIFIC LEGITIMATE FERTILITY RATES, SWEDEN.

Age-groups.	1936–40.	1941–45.
20–25	223	190
25–30	155	125
30–35	107	81
35–40	64	46
40–45	27	15
45–50	2	0

The exceptional course of the 15–20 group, omitted from Table X, adds to the uncertainties of prediction. Like the older age-groups, this young group has a relatively small effect on the total fertility, so that an approximate estimate is not likely to introduce any very large error as far as prediction of the total birth-rate is concerned. In passing, reference may be made to the somewhat similar situation which was found in connection with the death-rates. In that case the infantile mortality deviated from the general diagonal law in much the same way as the fertility of the group 15–20 does in the birth-rate tables. The analogy is, of course, a purely formal one, but is perhaps sufficiently curious to deserve notice.

SPECIFIC LEGITIMATE FERTILITY RATES IN ENGLAND AND WALES.

The data required for calculating the specific fertility rates for Great Britain do not exist, and, as far as the past is concerned, the loss is irremediable. Any attempt to arrive at estimates of what these rates actually were must depend in some degree on conjecture and analogy, and, at best, only an approximation to the facts can be hoped for. Indeed, it is only the urgency of shedding all possible light on the spectacular fall in the birth-rate which justifies any attempt to reconstruct a table of fertility rates for the last fifty or sixty years. Several authors, for example Rich (1934) and Honey (1937), have already made assumptions, usually highly speculative, in order to allow them to reach some conclusions as to the changes in progress in the specific fertility rates. It is natural to inquire whether the new diagonal law may not substantially assist in the solution of the problem. There seems to be nothing inherently improbable in the assumption that it holds for Britain as well as for the Scandinavian countries. It was therefore decided to take this law as the basis of the following computation.

It is first necessary to decide upon a series of standard rates, representing the fertility before the decline in the birth-rate began. In the case of Scotland, the well-known data for the year 1855 are available. In this, the first year of the complete registration of births in Scotland, the schedule to be filled up required information, *inter alia*, on the mother's age, and the figures have been fully analysed by Lewis and Lewis (1906) in a valuable memoir. The specific legitimate fertility rates for Scotland for this year are as follows:—

Age-groups .	15–20	20–25	25–30	30–35	35–40	40–45	45–50
Rates . .	511·2	427·0	366·0	302·4	242·0	113·3	18·1

As one might expect, these rates for Scotland do not differ very markedly from the standard rates for Denmark and Sweden given above (Tables II, IV). It is very probable that the rates for England and Wales agreed closely with those for Scotland. One simple test may be applied. The numbers of married women in quinquennial age-groups for the census years 1851, 1861, and 1871 are known, and so the total numbers of legitimate births may be calculated corresponding to any particular set of fertility rates. The Scottish fertility rates, applied to the English married women, give the following results:—

ENGLAND AND WALES.

Census Years.	Legitimate Births Observed.	Legitimate Births Calculated from Scottish Fertility Rates, 1855.	Ratio: Observed / Calculated.
1851	573,865	582,039	0·9860
1861	652,249	673,500	0·9684
1871	752,653	759,053	0·9916

The mean ratio of observed to calculated births is 0·9820. (It should be remarked that the Scottish rates refer to confinements, not children born, so that the calculated numbers of births should be increased by about 1% to allow for multiple births; but for the present purpose this point is not of great importance.) In the light of the above it seemed justifiable to choose, as standard for England and Wales, the rates obtained from the Scottish figures by multiplying each by 0·982. These modified rates are as follows:—

Age-groups	15–20	20–25	25–30	30–35	35–40	40–45	45–50
Rates	502	419	359	297	238	111	18

Finally, it is necessary to decide through what points the diagonals are to run. The definite facts of observation, which the scheme must agree with, are the numbers of total legitimate births as observed in the census years. (It is only in the census years that the numbers of married women in the various age-groups are known, and these numbers are necessary for the calculation of the total legitimate births from the specific legitimate fertility rates.) This alone is insufficient to fix the position of the diagonals without some knowledge of the relationship between them.

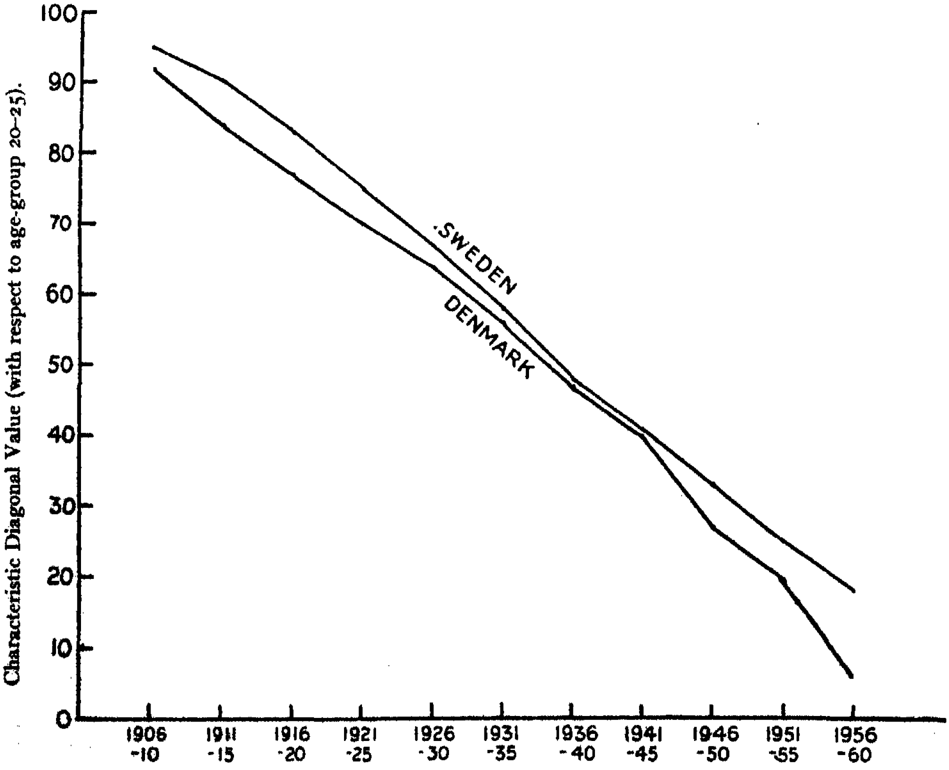


Fig. 1.

The various diagonals are each characterised by one figure, namely, the average of the relative fertility rates along the diagonal. For any particular age-group the various calendar years are each characterised by the value of the diagonal which passes through that year. If these characteristic values are plotted against the corresponding years at which the periods are centred, the points are found to lie, to a first approximation, along a straight line. It is obvious that the result will be independent of the particular age-group chosen. Fig. 1 shows the lines obtained for Sweden and Denmark.

If this linear relationship be taken as substantially correct, then the whole set of diagonals for any one country depends on only two constants, namely, those which, for any specific age-group, define this linear relationship. The problem is, then, to find the two constants which best fit the recorded numbers of births.

One minor difficulty remains. We have already seen that in Sweden and Denmark, and indeed in every country studied, the fertility of mothers under twenty follows an abnormal course. Fortunately, owing to the small number of married women in this age-group, the total number of births derived from it is relatively small, and it is sufficient to make a rough allowance for its contribution to the total births. We have therefore assumed that in England and Wales it has remained constant at its standard rate—an assumption certainly not true, but, in all probability, sufficiently accurate not to interfere seriously with the calculation of the other fertility rates.

TABLE XI.—CALCULATED RELATIVE SPECIFIC LEGITIMATE FERTILITY RATES, ENGLAND AND WALES.

Age-groups.	Standard Period.	1881.	1891.	1901.	1911.	1921.	1931.	1941.	1951.
15–20	100	100	100	100	100	100	100	100	100
20–25	100	100	100	95·5	82·5	69·5	56·5	43·5	30·5
25–30	100	100	100	89	76	63	50	37	24
30–35	100	100	95·5	82·5	69·5	56·5	43·5	30·5	17·5
35–40	100	100	89	76	63	50	37	24	11
40–45	100	95·5	82·5	69·5	56·5	43·5	30·5	17·5	4·5
45–50	100	89	76	63	50	37	24	11	0

The method adopted to obtain the two constants was one of trial and error. In this way it was found that diagonals, spaced at distances of 6½%, and having the locations indicated in Table XI, best accounted for the observed numbers of legitimate births in the census years from 1881 to 1931, excluding 1921 when the conditions were quite abnormal. The calculated specific legitimate fertility rates are then as given in Table XII, and the births, obtained by applying these rates to the observed numbers of married women in the appropriate age-groups, are shown in Table XIII. The observed numbers are given for comparison.

TABLE XII.—CALCULATED SPECIFIC LEGITIMATE FERTILITY RATES, ENGLAND AND WALES.

Age-groups.	Standard Period.	1881.	1891.	1901.	1911.	1921.	1931.	1941.	1951.
15–20	502	502	502	502	502	502	502	502	502
20–25	419	419	419	400	346	291	237	182	128
25–30	359	359	359	320	273	226	180	133	86
30–35	297	297	284	245	206	168	129	91	52
35–40	238	238	212	181	150	119	88	57	26
40–45	111	106	92	77	63	48	34	19	5
45–50	18	16	14	11	9	7	4	2	0

TABLE XIII.—COMPARISON OF OBSERVED AND CALCULATED LEGITIMATE BIRTHS.

Census Year.	Observed.	Calculated.	Percentage Error.
1881	840,522	837,163	- 0·40
1891	875,376	878,881	+ 0·40
1901	893,608	905,967	+ 1·38
1911	843,505	831,195	- 1·46
1921	810,196	721,323	- 10·97
1931	603,995	602,331	- 0·28

Tables XI and XII have been extended to include the years 1941 and 1951. It will be of interest to discover in due course how closely these predictions agree with the facts.

Fig. 2 gives the observed yearly numbers of births from 1851 onwards. The continuous line is drawn through the calculated points for the census

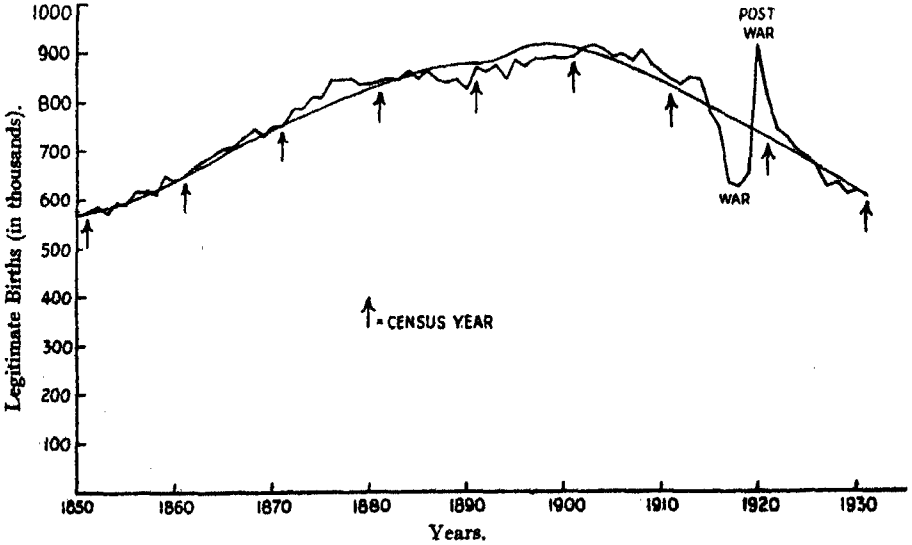


FIG. 2.

years 1851, 1861, etc., up to 1931. It must be remembered that, apart from the census years, the actual numbers of married women in the various age-groups are not known. In reality, they vary somewhat from year to year, and allowance for this variation is not possible in the inter-census years. Part of the deviation of the observed from the calculated for these years is doubtless due to this cause. The large disturbance during and after the War is evident, and it is clear that this effect accounts for the considerable discrepancy in 1921.

The fertility rates in Table XII are admittedly based on somewhat hypothetical assumptions, but one direct test may be applied. It happens that in 1921 and 1931 the Registrar-General for England and Wales, on the basis of the censuses for these years, attempted to deduce the fertility rates. The deduction of these rates from the census data involves certain assumptions not altogether beyond criticism, but they are the best direct estimates available. Actually, the Registrar-General issued two estimates for 1921, one in 1922, and a revised version ten years later. These estimates for 1921 and 1931 are given in Table XIV.

Table XIV.—Comparison of Specific Legitimate Fertility Rates as calculated by the Registrar-General (1921 and 1931) and as deduced in the Present Investigation.

Age-groups.	Registrar-General, 1931.	Estimated Rates as in Table XII, 1931.	Percentage Divergence.	Registrar-General, 1921 (*issued 1922*).	Registrar-General, 1921 (*issued 1932*).	Percentage Divergence.
20–25	267	237	− 11	359	334	+ 7
25–30	187	180	− 4	268	260	+ 3
30–35	127	129	+ 2	197	194	+ 2
35–40	81	88	+ 9	131	130	+ 1
40–45	33	34	+ 3	32	56	− 43

It will be seen that the discrepancies between the Registrar-General's estimates for 1931 and our own are of the same order as those between the two official estimates for 1921.

Another method of obtaining an approximate idea of the error likely to affect the estimates of the specific legitimate fertility rates given in Table XII is to apply the same procedure, based on the diagonal law and on the assumption of the linear relationship between successive diagonal values, to Sweden or Denmark. When this is done for Sweden the discrepancies between the calculated and observed values are found to vary from −9% to +16% of the actual, 30 out of 45 lying between −5% and +5%. The mean error (irrespective of sign) is 4·6%, and the root mean square error, 5·9%. Sweden, of course, is one of the countries in which we have found by our analysis that the diagonal law approximately holds; but when this agreement of observed and calculated is taken in conjunction with the range of the discrepancies shown in column 4, Table XIII, it is reasonable to conclude that the mean error involved in Table XII is probably of the order of 5%.

SUMMARY.

1. The method of analysis previously applied to the specific mortality rates of England and Wales, Scotland, and Sweden, has been applied to the specific fertility rates of Sweden, Denmark, and Finland. When, in any country, the specific fertility rates for any age-group (except those for 15–20) are expressed as percentages of the standard specific fertility rate for the same age-group (the standard rate referring to a period preceding the general fall in the birth-rate) the resulting percentages exhibit certain regularities, briefly described as conformation to a *diagonal law*. This law holds, approximately, both for the specific total fertility rates and for the specific legitimate fertility rates, except that in the former case the age-group 20–25 is somewhat exceptional, as well as the age-group 15–20.

2. The decline in fertility first influenced the older age-groups, and then gradually affected the younger women, the wave of reduction proceeding down the age-groups at the average rate of one year of age per calendar year. In the case of mortality rates the change was found to be the same in velocity, but opposite in direction—that is, the wave was associated throughout life with one and the same group of individuals.

3. The statistics for Norway and France, though less complete, reveal similar tendencies. In Finland, during and immediately after the War, and in France, during the War and in the post-War years, definite deviations from the diagonal law are observed.

4. On the basis of the diagonal law and certain other plausible approximate assumptions, estimates have been arrived at of the fertility rates in England and Wales for 1871 onwards. It is emphasised that these estimates are, at best, only approximate. They show a reasonable agreement with the Registrar-General's estimates based on the 1931 census figures.

We wish to express our thanks to Dr Methorst, Director of the International Institute of Statistics, The Hague, and to the authorities in the Department of Statistics, Copenhagen, the Central Bureau of Statistics, Helsinki, and the Central Bureau of Statistics, Stockholm, for helping us to obtain the fundamental data required in the above investigation. We are especially indebted to Mr A. McKinlay, Staff Officer in the Registrar-General's Office, Edinburgh, for much valuable assistance.

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(*Issued separately May* 5, 1938.)

VI.—The Sex Ratio of the Domestic Fowl and its Bearing upon the Sex-linked Lethal Theory of Differential Mortality. By **Professor F. A. E. Crew,** M.D., D.Sc., Institute of Animal Genetics, University of Edinburgh.

(MS. received November 19, 1937. Read November 8, 1937.)

OF the explanations advanced in respect of the observed inequality in the viability and longevity of the sexes in man, the sex-linked lethal theory advocated by Lenz (1923), Gunther (1923), Geiser (1924–5), Huxley (1924), Schirmer (1929), amongst others, has attracted most support. One reason for this is undoubtedly that it is a genetic theory promulgated at a time when biological thought was being profoundly influenced by the many spectacular discoveries which had been made in this particular science.

The action of sex-linked lethal genes is so dramatic in those instances in which their presence has been disclosed that it was but inevitable that their aid should be invoked also to explain the lesser viability of the heterogametic sex in other forms, even though in these such genes had not been identified. Furthermore, this theory had always assumed, in advance of ascertained knowledge, that it would be found on examination in the case of birds and moths, forms in which the female is the heterogametic sex, that the female would prove to be more fragile and less viable, to suffer more easily and more severely when exposed to unfavourable conditions, and to be removed from the population at most, if not at all, ages in relatively greater numbers.

If in those forms with male heterogamety it is the male, and in those with female heterogamety it is the female, that is less viable and particularly if in the former group the sex ratio swings from high to low and in the latter from low to high, then the sex-linked lethal theory must become unassailable. It is very necessary, therefore, that all reliable information concerning prenatal death, the secondary sex ratio and postnatal death in as many forms as possible, and especially in birds and moths, should be collected and made available until the whole question has been finally decided.

There is an abundant literature on the sex ratio of the fowl, and much of this has been summarised by Landauer and Landauer (1931) and by

Byerley and Jull (1935), between whom there is serious disagreement. The figures that these investigators gave are as follows :—

	Per cent. Males.	Deviation from 50 per cent.	Deviation / P.E.
Sex ratio amongst 24,853 dead embryos.	47·85 (Byerley and Jull)	− 2·15 ±0·21	10·2
Sex ratio amongst 67,993 live-born chicks.	48·77 (Landauer and Landauer)	− 1·23 ±0·13	9·5
Sex ratio amongst 96,008 live-born chicks.	49·17 (Byerley and Jull)	− 0·83 ±0·11	7·6
Sex ratio amongst those dying during the first eight weeks of postnatal life.	52·7 (Landauer and Landauer)	+ 2·7	...

Landauer and Landauer expressed the opinion that if any differential mortality during embryonic development occurs it is the male that suffers more, that there is a slight excess of females at hatching, and that more males than females die in the early weeks of postnatal life. Byerley and Jull, on the other hand, presented the view that if and when there is any differential mortality between the sexes more females than males die before hatching, that there is a slight preponderance of females amongst the live-born; they could find no evidence whatsoever of any differential postnatal mortality between the sexes. They look upon their figures as supporting the sex-linked lethal theory, whilst Landauer and Landauer, as also MacArthur and Baillie (1932), were of the opinion that theirs did not. When such competent and trustworthy observers as these disagree amongst themselves concerning such matters, this in itself is sufficient reason for further investigation.

Jull (1931) pointed out that there are significant differences in the secondary sex ratio for the fowl as reported by different investigators, whilst Callenbach (1929), and especially Byerley and Jull (1935), have shown that there are equally significant differences in the secondary sex ratio in different breeds. For example, they found that the sex ratio of their Rhode Island Reds was 52·6 ± 0·38 (P.E.) per cent. males, whereas that of their White Leghorns was only 48·2 ± 0·34 (P.E.). In view of these observations it became very desirable that the secondary sex ratio of as many different breeds as possible should be studied. It is probably quite wrong to speak of breed in this connection, for the term can have no real significance. "Breed" should always be interpreted as meaning "stock" or "strain."

In this country as elsewhere there is an enormously large industry concerned with the production and sale of day-old chicks of known sex. The methods of sex recognition employed in these commercial undertakings are: (1) the sex-linked, popularised through the pioneer work of Punnett; and (2) the Japanese.

The first makes use of the fact that certain plumage-colour characters in the fowl are sex-linked in their mode of inheritance. The commonest mating is that of a "gold" cock (*e.g.* Rhode Island Red) with "silver" hens (*e.g.* White Wyandottes or Light Sussex). The male offspring of these matings are white in the down colour, the females buff, and so the two are easily distinguished amongst the newly hatched. The Japanese method, which can be used also for sex recognition in pure breeds, is based upon the fact that the size (and in certain breeds and varieties the degree of pigmentation also) of the cloacal papilla are greater in the male than in the female. This method has been very largely exploited in Japan, where there are organised schools for the training of experts from whom is demanded an accuracy of at least 98 per cent., confirmed by dissection. At the present time there are in this country a number of such Japanese experts who are paid at the rate of so much for every chick that is sexed.

Wishing to obtain information of a magnitude that only the largest commercial firms could possibly supply, I turned to Messrs Thornber Bros. of Mytholmroyd, Yorkshire, and to Mr W. D. Evans of the Kibworth Hatchery, Leicestershire. Thanks to their interest and great kindness I have been permitted to examine their hatching records for the past season.

Those from Messrs Thornber Bros. deal only with two sex-linked crosses, and the identification of sex was made solely on the basis of down-colour differences (Table I).

From the same firm I obtained as a free gift and at considerable trouble to the donors, ten thousand incubated eggs, from the same mating, which had failed to hatch. From these I obtained 8565 dead-in-shell of a size that permitted their sex to be recognised by reference to down colour and by dissection (Table II).

All these ratios are very near equality, and as far as they go the figures seem to show that there is little, if any, sexually selective mortality in these stocks. If there is any, then apparently it is the male that is removed thereby. If there is but little prenatal sexually selective mortality then on general grounds (Crew, 1937), it is not to be expected that the secondary sex ratio would be far removed from equality. The figures for the secondary sex ratio in the stocks show that there is a slight but commonly a significant preponderance of males among the live-born.

It is interesting to note that the sex ratio amongst the dead-born and for the live-born progeny of these matings differ in the degree of their differentiation from the 1 : 1 ratio. A significant deviation amongst the dead-born is associated with a differentiation that is not significant amongst the live-born of the same mating, and *vice versa*. A considerable number of pens were involved in the parentage of these chicks, and consequently it does not follow that the live-born and the dead-born were derived from the same birds. Furthermore, the figures for the live-born and the dead-born respectively were obtained at different seasons of the year. Possibly in these facts is to be found the explanation of this somewhat puzzling difference.

TABLE I.

Parental Stock.	Total Live-born.	Total Males.	Percentage Males.	Deviation from 50 per cent.	Deviation
					S.E.
White Wyandotte hens × Rhode Island Red cocks	346,874	173,688	50·07	+0·07 ±0·08	< 1
Light Sussex hens × Rhode Island Red cocks	169,102	86,052	50·89	+0·89 ±0·12	7·4
Totals	515,976	259,740	50·34	+0·34 ±0·07	4·9

TABLE II.

Parental Stock.	Total Chicks.	Total Males.	Percentage Males.	Deviation from 50 per cent.	Deviation
					S.E.
White Wyandotte hens × Rhode Island Red cocks	5707	2936	51·45	+1·45 ±0·66	2·2
Light Sussex hens × Rhode Island Red cocks	2858	1435	50·21	+0·21 ±0·93	< 1
Totals	8565	4371	51·03	+1·03 ±0·54	1·9

Sex identification by reference to such sex-linked plumage-colour characters is both simple and exceedingly accurate, but I am not at all sure that the "Japanese" method yields results which can be accepted equally easily. It is true that the experts concerned are expected to be right in not less than 98 per cent. of instances. It may be assumed that in any doubtful case the chick is more likely to be classified as a male than as a female, since the demand is for day-old chicks guaranteed to be females. The figures for the sex ratio in the following Table (III) may therefore be somewhat inaccurate. The records in Table III are given because they are so very numerous and because, even when allowance has been made for possible inaccuracy, they still support the conclusions derived from the records in Table I.

TABLE III.—LIVE-BORN.

Parental Stock.	Total Chicks.	Total Males.	Percentage Males.	Deviation from 50 per cent.	$\frac{\text{Deviation}}{\text{S.E.}}$
Rhode Island Red	756·294	392·832	51·94	+1·94 ±0·06	32·3
Light Sussex	168,425	87,508	51·96	+1·96 ±0·12	16·3
Light Sussex × Rhode Island Red	299,272	153,001	51·13	+1·13 ±0·09	12·6
White Leghorn	137,609	69,617	50·59	+0·59 ±0·13	4·5
White Leghorn × Rhode Island Red	363,224	185,737	51·14	+1·14 ±0·08	14·3
White Wyandotte	99,485	53,539	53·82	+3·82 ±0·16	23·9
White Wyandotte × Rhode Island Red	353,531	177,158	50·11	+0·11 ±0·08	1·4
Black Leghorn	3,453	1,774	51·38	+1·38 ±0·85	1·6
Mixed	34,758	17,445	50·19	+0·19 ±0·27	< 1
Totals . .	2,216,051	1,138,611	51·38	+1·38 ±0·03	46

From the Kibworth Hatchery I obtained the original records for the seasons 1935–6 and 1936–7, each sheet of which was signed by the particular Japanese expert concerned. The recognition of sex in the majority of the stocks was based solely on an appreciation of the relative size (and degree of pigmentation) of the cloacal papilla. It will be seen (Table III) that the differentiation from the 1 : 1 ratio in five out of the nine progenies is highly significant, and that in every case without exception there either is, or possibly is, a real excess of males. The fact that all these progenies show a male preponderance points directly to the conclusion that in these figures in themselves there is no support whatsoever for the sex-linked lethal theory. It is to be noted also that the sex ratio varies from stock to stock, ranging from the 53·82 of the White Wyandotte to the 50·11 of the cross-bred White Wyandotte × Rhode Island Red. This observation is a confirmation of the conclusions of Callenbach, and of Byerley and Jull, and makes it probable that the differences in the secondary sex ratio as reported by different observers have no other meaning than that different observers have used different materials. Another point of interest is to be found in the fact that though the sex ratio of the cross-bred progeny of White Wyandotte hens × Rhode Island Red cocks shows no significant deviation from the 1 : 1 ratio, the deviation is highly significant in both of the parent stocks. In this observation perhaps lies a certain support for the idea that there are specific sex ratio genes in the fowl, as in other forms, which in their action influence the functioning of the heterogametic mechanism, leading to the production of the X- and Y-bearing gametes in unequal numbers, and that hybridisation can yield in the offspring a genotype which, in respect of these sex ratio genes, is different from that of either of the parental stocks (Crew, 1937).

The sex-linked lethal theory finds no support in the fact that of the dozen lethal genes that have been so far recognised in the fowl (Eaton, 1937) only one—recessive white, found in a White Leghorn stock by Upp and Waters (1935)—is sex-linked. The fowl is so extensively used as experimental genetical material that surely had there been many sex-linked lethals, more than one would have been identified.

SUMMARY.

1. The sex ratio among 8565 dead-in-shell and among 515,976 live-born "sex-linked" chicks together with that among 2,216,051 live-born, "sexed" by the Japanese method, offer no support for the sex-linked lethal theory which demands that the heterogametic female shall be less viable than the male.

2. Different "breeds" yield different secondary sex ratios, and in this fact probably lies the explanation of the different results obtained by different investigators.

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(*Issued separately May* 5, 1938.)

VII.—Studies on Reproduction in the Albino Mouse. I. The Period of Gestation and the Time of Parturition. By Hugo Merton (Heidelberg). *Communicated by* Professor F. A. E. Crew, M.D., D.Sc. (With Four Figures and Three Tables.)

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A. INTRODUCTION.

THE cellular processes of ovulation, maturation and fertilisation of the ovum in the albino mouse have been the subject of repeated and exact studies, and are now sufficiently well known. The biological phenomena of propagation in the mouse, *i.e.* the sexual cycle, œstrus, and copulation, have likewise been described in detail, but our knowledge concerning the period of gestation and the moment of parturition is still very inadequate.

In my attempts to master the technique of artificial insemination in the mouse it was found that this will be successful only if we have an exact knowledge of the different phenomena from copulation to parturition. It therefore appeared important to collect new data, firstly, on the appearance of the vaginal plug as a reliable sign of a preceding mating; in this connection the still open question, whether a conception is possible at each œstrum, could be elucidated. Secondly, new observations had to be made on the appearance of blood in the vagina during pregnancy. Thirdly, the variation in the weight of the ♀♀ during the different phases of pregnancy had to be accurately determined. The knowledge of these facts as well as their time relationship enabled us to predict with some degree of certainty at what time a birth is to be expected. But in order that artificial insemination may be successful it is not sufficient to estimate the time of birth only within 12–24 hr., and a recording apparatus had to be constructed which would give the time of birth to the hour. Such an apparatus allows us, amongst other things, to determine how the times of birth are distributed throughout the day. In connection with the observation of the time of the birth-act it appeared desirable to collect data on in how far the litters before and after birth are alike, and in what way the size of the litters varies in the different months.

I am greatly indebted to Professor F. A. E. Crew for his help and courtesy. I also wish to thank Dr J. M. Robson for calling my attention to several relevant papers.

B. Observations during Pregnancy.

1. *The Vaginal Plug.*—The plug found after successful copulation in the vagina of the ♀, if it reaches the external orifice, is easily recognised; an inner plug which does not come to the surface will have to be probed. In some cases the inner plug will only just cover the orifice of the cervix and often will be difficult to recognise. According to Sobotta, the plug is extruded at the earliest in 20 hr., at the latest in 30 hr. after mating; if the ♀♀ are examined only once in 24 hr., the plug may have disappeared. As the observation of the plug is the best starting-point for calculating the time of birth, it is advisable to examine the ♀♀ twice in 24 hr.

Generally the sexual cycle of the ♀♀ recurs every 4 days, and consequently the ♀♀ will mate after a period of 4 days; this was the case in nearly all the pregnant ♀♀. From this it may be stated that the sexual cycle in my stock occurred very regularly; according to my notes this took place with the same regularity in April–June as in December–February. Occasionally, especially in younger ♀♀, a plug can be found twice in the course of 4 days; in such cases no fertilisation seems to have occurred after the 1st plug or else the developing ova have perished owing to new ovulation, but in any case the day of birth is determined by the second plug.

2. *The Placental Sign.*—Long and Evans have found that in rats blood can be detected in the vagina from the beginning of the 3rd week of gestation. Parkes (1926) found the same "placental sign," as it has been called by Long and Evans, in mice. He states that it appears on about the 12th day of pregnancy, but does not give any details. It might be of interest to give further information on this subject. The amount of blood found in the vagina varies very much, but the bleeding appears

with great regularity and can be demonstrated macroscopically (by introducing the probe end and taking the smear on filter paper). 37 amongst 44 ♀♀ showed bleeding first between the 8th and 6th day before parturition, *i.e.* on the 11–13th day of pregnancy; in 24 cases this occurred on the 7th day. In 7 cases only bleeding took place earlier than 8 days before parturition (5 instances), or less than 6 days (2 instances). Although the calculation of birth by observation of the plug is more exact, the placental sign is rather important if no plug has been found, or if its presence was uncertain. In such cases it is advisable to examine the vaginal contents if sufficient time has passed after a possible copulation and when a first enlargement of the body is noticed.

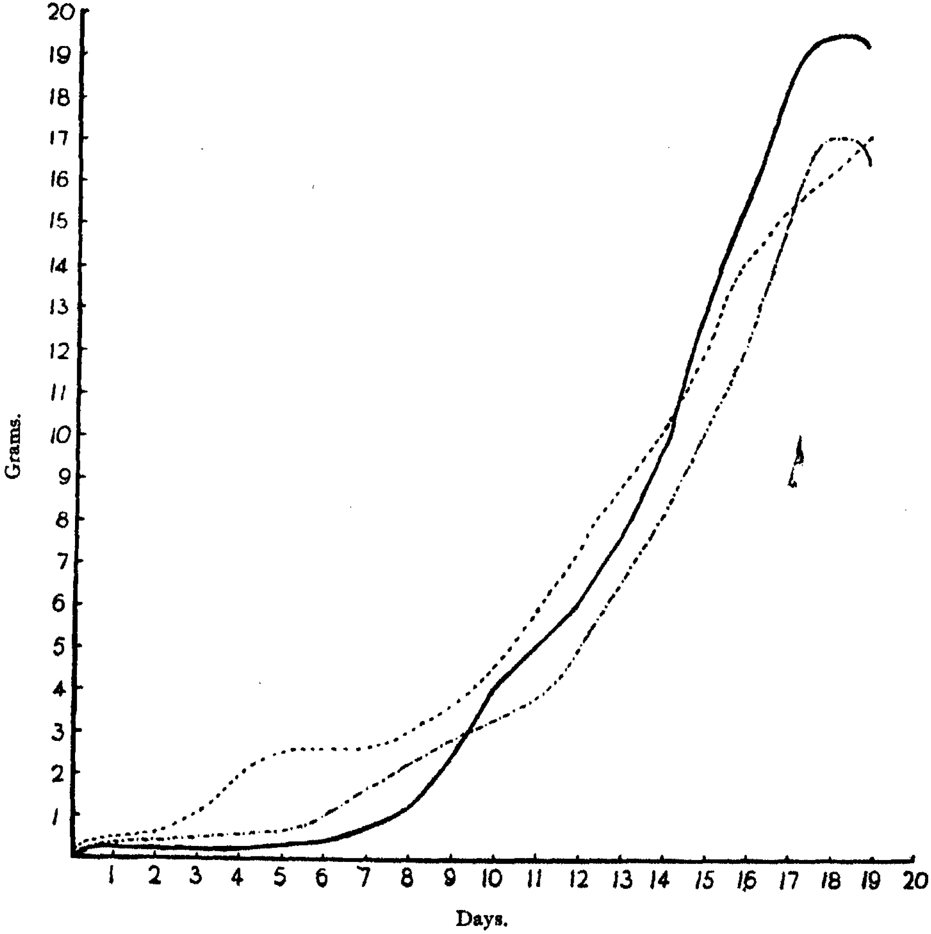

FIG. 1.—Curves of the absolute weight increase of 3 ♀♀ during pregnancy.

3. *The Increase in Weight during Pregnancy.*—During the first 3½ days the developing ova pass through the oviducts, and implantation occurs only at about the end of the 5th day; an increase in weight therefore can be expected only when the preparatory changes in the uterus have begun. The increase in weight observed during the first 8 days, on the average of 1–2 g., occurs chiefly during the 2nd part of this period. The accelerated growth of the placentæ and the developing embryos during the following period, beginning with the 9th and ending with the 12th day inclusive, is expressed by a greater increase of weight, *i.e.* 3–5 g. From the 13th to the 18th day growth rate is highest, the weight of the ♀ increasing from 6 g. to 13½ g., according to the size of the litter, which means a daily increase of 2 g. or more. The 3 curves of weight in fig. 1 demonstrate the actual observed increase in 3 pregnant ♀♀; to permit comparison, all curves are based on the absolute weight increase.

A ♀ can thus nearly double her weight during pregnancy, though this will only be the case for ♀♀ pregnant for the 1st or 2nd time and weighing 18–23 g. Older ♀♀ in my stock which had been pregnant several times weighed 26–31 g. when non-pregnant and not more than 46–48 g. during pregnancy.

The knowledge of the variation in the weight increase during the different periods of pregnancy provides us with another method of finding out whether a mouse has been fertilised and how far pregnancy has advanced—namely, by weighing on different days.

C. THE TIME OF PARTURITION.

4. *A Self-recording Balance for determining the Hour of Parturition.*—There are two spheres in the biology of reproduction of the mouse where it may be desirable to know the moment of parturition as exactly as possible. As the ♀♀ come on heat during the first 24 hr. after parturition, and therefore can be fertilised during this time, it may be important to know on the average how many hours after parturition ovulation occurs, and to find out during which period fertilisation may take place. The knowledge of these processes and possibilities is the necessary prerequisite for successful artificial insemination, which will be referred to in a following publication.

Secondly, an exact knowledge of the hour of parturition is necessary if it is desired to establish whether, for instance, there exists a relationship between the duration of gestation and the number of young, or how the births are distributed throughout the day.

If dealing with a fairly large material, it is impossible to state by direct observation the hour of parturition for each single ♀, and it will be necessary to use an apparatus which will register this process automatically. Most of the authors were satisfied with examining all the cages every morning, and where they found fresh litters they assumed that birth had taken place during the night. We shall see later that this is by no means the case.

It is obvious that for such a self-recording apparatus a balance with lever-arms of different length should be fitted, as, for instance, the old letter-balance. The following change had to be introduced in such a letter-balance. Instead of the letter pan there is a cage-bottom made of a tin sheet 20 cm. square bordered by a vertical tin strip about 3 cm. high. All changes of weight on the floor of the cage are registered by a pointer on the drum of a kymograph which is attached to the vertical stand that supports the floor of the cage. An adjustment must be made on the other lever-arm which carries the weight for the weight to slide on the scale beam. The shorter beam carrying the cage-bottom must be slightly raised before the pregnant mouse (weighing 33–45 g.) is placed into the cage. The remaining parts of the cage, *i.e.* the sides and the top, are held by 4 supports, which are fixed on a square base and are immovable while the cage-bottom swings up and down (fig. 2). The space between

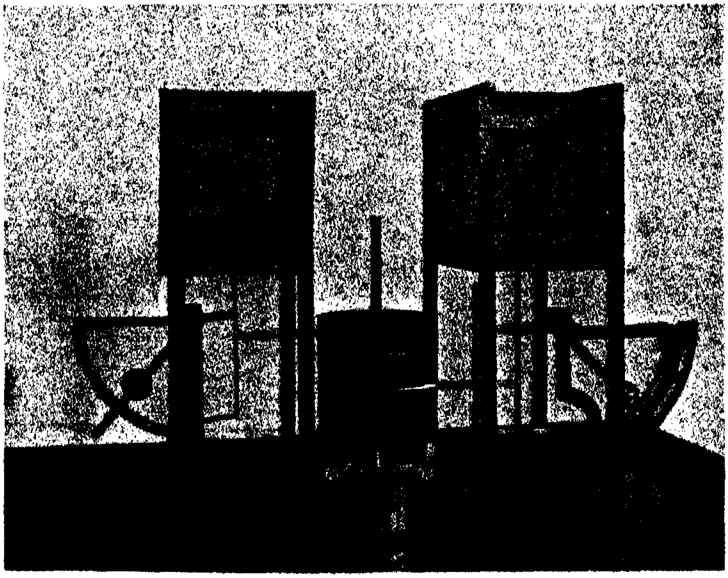

FIG. 2.—Two self-recording balances registering all weight changes on the drum of a kymograph.

the bottom and the sides must be only a few mm., to prevent the mouse from escaping. The almost horizontal position of the shorter lever-arm, as described above, is therefore desirable, because the lateral displacement of the floor during lifting and lowering of the cage-bottom is reduced to a minimum.

Only in this way will changes in weight be clearly registered on the kymograph by lines which are traced at right-angles. A small tin tray is fixed along one side of the cage about 5 cm. above the lower border. This carries the bowls for food and milk, fixed so that they cannot be dragged to the cage-bottom. At first, when they were fixed higher, some mice were afraid to step on to the tray, because they could not get to it in one leap from the swinging bottom. In order to diminish the swaying motion of the floor when the animals are leaving or returning, the following adjustment was made. A curved metal strip with a longitudinal slit was attached to the supporter on the side of the beam carrying the weight, and two screws were fixed in this slit in such a way that one corresponded to the loaded, the other to the unloaded, position of the balance. This arrangement renders the graph clearer, because all lines beyond the stops are eliminated in passing from one equilibrium to the other. In one corner of the cage-floor there is a little open tin box filled with loose wool; it was regularly used for nest-building.

Subsequently the letter-balance was discarded, and instead an exact weighing apparatus was used. This was mounted on a base in such a way that the rod carrying the cage-floor was exactly at the point of intersection of the two diagonals connecting the 4 cage-supports.

5. *The Records of the Balance and their Interpretation.*—The following changes in weight can be observed from the curve on the drum of the kymograph. (1) The difference in weight of the pregnant mouse on the floor of the cage or away from it, *i.e.* the curve shows a rise for the time when the ♀ is on the feeding tray or runs about along the walls of the cage. (2) After the mouse has littered, the weight of the litter on the floor of the cage is recorded continuously even if the mother is not there. Consequently the curve now rises less than before parturition; but every time the mother leaves, the pointer at the first movement will swing beyond the equilibrium, and therefore these curves show on the left side of the rectangular curve a vertical line rising above the level (fig. 3). It may happen that there will be no such line, when the friction between the pointer and the drum is a little too great, but nevertheless the different height of the rises before and after birth can always be recognised. Besides these changes in weight, the curve shows the frequency and duration of the absence of the ♀ from the cage-bottom, and

these time indications are especially important for recording the exact time of parturition.

The curves vary according to the temperament of the mice. Some mice stay on the tray for 5 or 10 min. at intervals of about 1 hr., others carry away each single grain, eating it in their nest. Some mice manifest the nest-building instinct by an unrest of several hours when the tray is visited and left repeatedly. When parturition is approaching, the pregnant ♀ stays in the nest. It is during this "birth pause," as we will call it, which lasts on an average 4–5 hr., that the young are born. Occasionally similar long feeding pauses can be observed without parturition taking place, but they can always be recognised. Sometimes a pause of several hours may follow after the first food-taking after parturition.

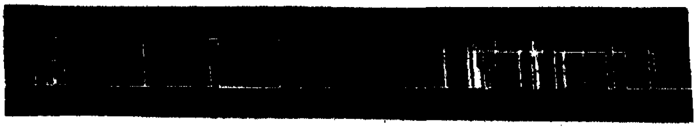

FIG. 3.—Kymographic record of the ♀ during parturition. On the left side rises before birth, on the right side after birth. The duration of the "birth pause" has been reduced (dotted line).

The birth pause is only partly occupied by the act of birth itself. During parturition the mother is eager to devour all the placentæ and the embryonic membranes, but the pause lasts considerably longer than would be necessary for this to take place; this can be explained by the mother being exhausted through labour and occupied by cleaning and nursing the young ones, and also by the fact that her hunger has been appeased for the moment after devouring the placentæ. It may happen that during this pause one or two of the young are eaten up, though this happened relatively seldom in my stock, as I have observed in quite a number of ♀♀ by counting the number of implantations in the uterus.

Among 100 births which have been registered, the average duration of a birth pause was found to be 276·8 min., or about 4⅔ hr. In 10 cases the pause was under 200 min. (the shortest was 126 min.), and in 9 it was over 400 min. It is not quite certain whether the long birth pauses may be regarded as equivalent of the others, as it is possible that birth may follow after a longer resting pause. Generally parturition begins at the latest one hour after the commencement of the pause. If we omit the 9 births with over 400 min., the average time for the remaining 91 is 4⅓ hr. Among the above-mentioned 100 litters, for 41 with a preponderance of ♂♂ we find an average pause of 290·2 min.; for 12 litters with an equal distribution of the sexes, of 283·8 min.; and for 42 with a preponderance of ♀♀, of 266·2 min.

The average duration of the pause for large litters with 10–12 young (25 instances) is 268 min., for small litters with 4–6 young (16 instances) 284 min.—just the contrary of what one would expect. I have the impression that if the litter is large, parturition is assisted by the greater tension of the body-wall.

Table I shows records of 33 births grouped according to the duration of the birth pause, the size of the litter, the sex-ratio, and the number of the litter. As there is no difficulty in recognising the sex of the new-born, the few cases in which the sex could not be decided refer to young which had been partially eaten.

TABLE I.—THE DURATION OF THE "BIRTH PAUSE."

No.	Serial No.	Hours, Minutes.	Minutes.	Litter Size.	♂♂.	♀♀.	Litter No.	Remarks.
1	43*c*	5 0	300	9	6	3	I	
2	,,	6 56	416	4	3	1	III	
3	,,	5 50	350	10	3	7	IV	
4	,,	2 34	154	12	7	5	V	After 10 min. 1st young.
5	18*b*	4 0	240	11	5	6	IV	,, 20 ,, 1 young.
6	26*b*	3 54	234	9	4	5	I	,, 30 ,, 1 young.
7	25*c*	2 24	144	12	5	4	..	,, 30 ,, beginning.
8	49*a*	3 4	184	9	5	6, 1?	IV	,, 24 ,, 1 young.
9	,,	4 30	270	9	4	5	V	
10	,,	8 14	494	7	3	4	VI	
11	60*a*	7 2	422	5	2	3	IV	
12	,,	3 38	218	5	2	3	V	,, 30 ,, 4 young.
13	2	3 24	204	9	3	6	I	,, 48 ,, 5 young.
14	25*b*	4 40	280	10	3	7	I	
15	,,	4 6	246	9	3	6	II	
16	,,	3 24	204	5	2	3	III	
17	,,	7 42	462	10	6	4	IV	
18	11	4 50	290	9	7	2	..	,, 55 ,, 6 young.
19	,,	5 20	320	8	4	4		
20	51*b*	6 0	360	8	3	5	II	After 102 min. all young present.
21	,,	4 40	280	10	8	2	III	
22	,,	7 42	462	6	1	5	IV	
23	46*a*	4 26	266	7	3	4	II	
24	,,	4 0	240	10	4	6	III	After 125 min. 9 young.
25	75*d*	6 40	400	12	2	10	III	
26	18*c*	3 54	234	12	8	4	III	,, 40 ,, beginning.
27	25*a*	4 20	260	8	3	5	I	,, 45 ,, beginning.
28	17*a*	4 0	240	8	5	2, 1?	V	After 50 min. 2, after 75 min. 4, after 130 min. 6 young.
29	32*a*	4 25	265	8	6	2	I	
30	,,	2 45	165	11	7	4	II	After 60 min. no young, after 95 min. 9 young.
31	,,	3 48	228	9	4	5	IV	
32	58*c*	3 16	196	9	4	5	II	
33	,,	2 6	126	7	5	2	V	

The records have been selected so as to compare the most widely different litters from the same ♀, and to demonstrate whether there exists a relation between the duration of pause and the size of litter; no evidence has been found for this. For all that, it seemed to me of importance to summarise these observations and to mention the findings concerning the beginning and duration of parturition in relation to the total birth pause.

The first young may be born 10 min. after the beginning of the pause. Usually it appears after about 30 min., at the latest about an hour after the beginning of the pause. The second young follows after a shorter or longer interval, whilst the remainder generally follow more rapidly. In the case of ♀♀ in which parturition is easy, the whole litter may be present after half an hour's time, while in others which have difficulties the process may last at the maximum 3 hr. All the records of mice of my own two stocks, as well as of animals bought from two commercial breeders, agreed in regard to the birth pause and the duration of the act of parturition. This fact should be stressed, as my findings in this respect are rather different from the observations of Long and Mark. On the basis of my own observations during the act of parturition and the records of the self-recording balance, I have determined the following time relationship: if the pauses were below 4 hr., the beginning of parturition was assumed to occur 30 min. after the beginning of the pause; in pauses of 4–6 hr., after 45 min.; in those longer than 6 hr., after 1 hr. In this calculation the difference between the assumed and the actual beginning of parturition never amounts to more than 45 min., and is generally less.

6. *The Moment of Copulation and the Duration of Pregnancy.*—The duration of pregnancy in albino mice is generally stated to be 19 days. It is difficult to observe the time of mating, as often several hours may pass after the sexes have been brought together before the final copulation takes place.

I succeeded in registering exactly the time of the last copulation by using a modification of the recording balance. This is possible, because after the final copulation no further attempts at mating are undertaken. I will not describe this construction here, as the time is known with a sufficient degree of accuracy if the sexes are brought together for only 2 hr.

As is well known, it cannot be assumed with certainty from the appearance of cornified cells in the epithelium of the vagina that an ovulation will follow, for the oocytes may become atretic so that not every fertile mating need be successful. I have a definite impression that the reason why in literature atresia is stated to occur so often is that the experimental material was in a poor state of nutrition or had just been procured from a commercial breeder. If the interrupted cycles were as frequent as it has been stated, then the following results with my stocks over a limited space of time would not be possible. Of 90 ♀♀ for which all events since birth were recorded on cards, during the months of April–August 84 were fertilised successfully during the 1st œstrus, after they had been together with a ♂. Of the 6 remaining ♀♀, 4 (Nos. 70*a*, 70*b*, 70*d*, and 68*b*) were fertilised only during the next fortnight; of these Nos. 70*a*, *b*, and *d* were sisters, and their delayed fertilisation may have a genetical basis. Of the 2 remaining ♀♀, 60*b*, 6½ months old, had never had a normal parturition and had only once aborted, and 66*a* was not fertilised during 18 days, although she had produced several litters before. Therefore atresia can be assumed only in 2, or at the most in 5 ♀♀ amongst 90. I do not possess sufficiently exact figures for other months of the year, but up to now I have the impression that atresia is rare during the cold season if the mice are kept in a warm room; it occurs mostly in October, the month which corresponds to the end of the original breeding season. Of course, by this I do not want to dispute the fact that some of the oocytes in the course of maturation may not be expelled and will become atretic and atrophy. As the figures given above demonstrate, there is a very good chance that a fertile mating will occur during the 1st œstrus after the sexes have been placed together. More failures are to be expected when they remain together for only 2–3 hr., even if the different stages of the œstrous cycle can be distinguished exactly by the presence of cornified cells. But if ♀♀ which have just littered are brought together with a ♂ for only 2 hr. during the first 24 hr. after parturition, fertilisation will take place in this short space of time. According to Sobotta, this heat period appears in the course of the first 24 hr. after parturition, and according to Allen between the 6th and the 24th hr. The results of the present investigation confirm Allen's findings; once the peak of the heat period has been reached it persists for a number of hours. If, therefore, we want to determine the exact time of pregnancy it is advisable to use such ♀♀. This has been done to get the observations which are shown in Table II. As far as copulation was observed directly, the exact time could be inserted in the table; if this was not the case, half of the 2-hr. period was assumed to be the moment of copulation. In such instances the letter "*c*" was inserted in the column "copulation" before the figure, and similarly in the column "duration of pregnancy." The duration of pregnancy in these 6 ♀♀ shows a deviation of 1 day and 6 hr., with a mean of 19 days and 4 hr. No correlation appears to exist between the duration of pregnancy and the size of the litter.

TABLE II.—EXACT DATA ON THE DURATION OF PREGNANCY.

Serial No.	Copulation.		Birth.		Duration of Pregnancy.	Litter.	♂♂.	♀♀.	Preceding Litter.	♂♂.	♀♀.
	Day.	Hour.	Day.	Hour.							
32*a*	10.V	11.45 p.m.	29.V	7.30 p.m.	18 days 20 hr.	11	7	4	8	6	2
71*c*	18.V	*c*1.00 p.m.	6.VI	9.00 a.m.	18 ,, *c*20 ,,	9	7	2	8	5	3
73*b*	17.V	12.00 noon	5.VI	1.00 p.m.	19 ,, 1 ,,	8	5	3	7	5	2
75*a*	23.V	12.00 noon	11.VI	2.00 p.m.	19 ,, 2 ,,	10	4	6	7	5	2
71*d*	21.V	*c*8.20 p.m.	10.VI	1.00 a.m.	19 ,, *c*5 ,,	7	2	5	8	5	3
78*a*	25.V	*c*11.00 p.m.	14.VI	1.00 a.m.	20 ,, *c*2 ,,	9	6	3	9	5	4
						54	31	23	47	31	16

7. *The Distribution of Births throughout the Day.*—As there may be a difference in duration of pregnancy of 1–2 days in either direction, there seems to exist no physiological reason for preferring any special time of day, although it is quite possible on phylogenetic grounds that originally parturition in mice occurred during the night. In literature on albino mice, night is given as the time of parturition.

The results of my observations with the aid of the recording balance show, as demonstrated by fig. 4, that during the time from 8 p.m. to 8 a.m. the number of parturitions is highest from midnight to 4 a.m., and then falls off very rapidly. Gradually a second rise is reached again at the time between 4 and 8 p.m., but surprisingly the number of parturitions decreases again between 8 p.m. and midnight. 164 parturitions were recorded. The number of parturitions from 8 p.m. to 8 a.m. and that of parturitions between 8 a.m. and 8 p.m. were equal, viz. 81:83. The figures for the 12-hr. period in which the 2 maximæ were found, viz. from 4 p.m. to 4 a.m., as compared with the remaining 12 hr., when the numbers of parturitions is lower, give a ratio of 110: 54, or 2: 1. The decrease between 8 p.m. and midnight, *i.e.* between the 2 maximæ, is remarkable; it may be that it would disappear in working with larger numbers, or it might be a peculiarity of my stocks. I am not including the results with 132 earlier records, as those records were not quite reliable.

8. *The Size of Litter and its Control.*—In a former section we have found how great may be the increase in weight of the ♀♀ during pregnancy. To a certain degree it is possible to deduce the size of the litter from the difference between the weight at the beginning and the end of gestation. This will always be rather difficult, especially in first litters when the young are generally very small. MacDowell and Lord have proceeded to find out, by counting the corpora lutea during the last week of pregnancy, how far an agreement exists between the litter size and the number of eggs.

expelled at the last ovulation. It is obvious that eggs may perish at the time of fertilisation and later on at implantation, and that some may die during embryonic development; finally, young may be eaten during the parturition.

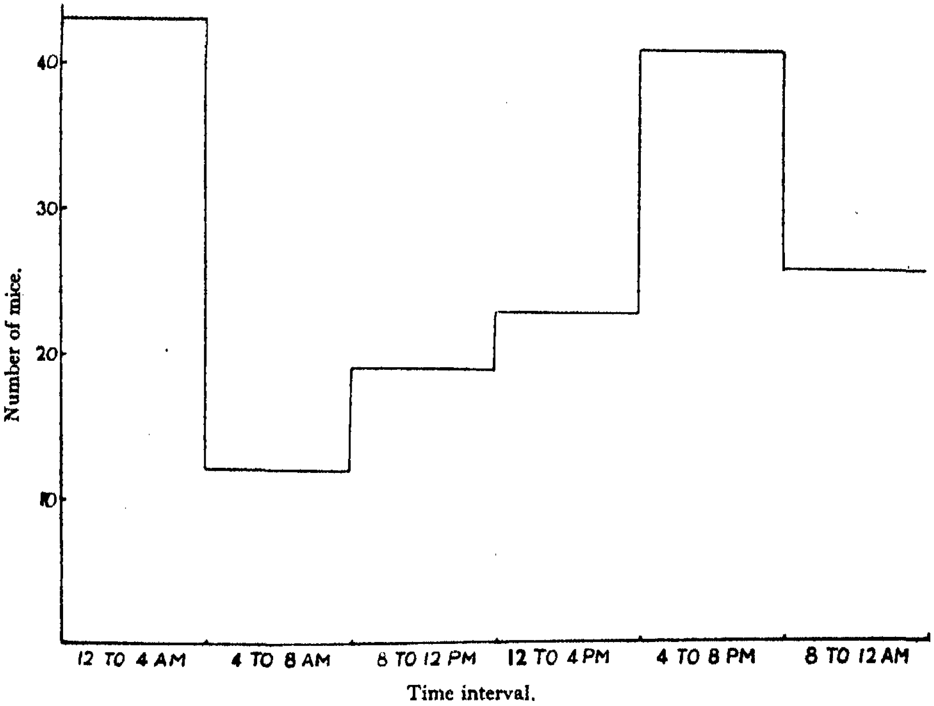

FIG. 4.—The distribution of parturitions of 164 ♀♀ throughout the day, as recorded by the self-recording balance.

In order to determine how many young had disappeared during parturition the uteri were examined 18–24 hr. after parturition in a number of ♀♀ and the number of implantations compared with the number of young found. From the following table (III) it will be gathered that the proportion of missing young is small; it amounts to 2½ per cent. In one case 2 ova must have become implanted at the same place. Weight records show that it is permissible to conclude that the litter is complete only if the difference between the weight of the mother before parturition and after parturition plus the weight of the litter is small. Of course the weighing was done as soon as possible after parturition, but as these observations were made at a time when the recording balance was not yet in use, it is possible that some of the ♀♀ might have taken some food before, though the rather high weight difference between columns I and

TABLE III.—WEIGHT BEFORE AND AFTER BIRTH, NUMBER OF IMPLANTATIONS, AND NUMBER OF EGGS IN OVIDUCTS.

No.	Weight.					Litter and Uterus.				Eggs in Oviducts.	
	Female.										
	Before Birth. I.	After Birth. II.	Litter. III.	Female and Litter. IV.	Difference between I and IV. V.	Litter Size. VI.	Right Uterus. VII.	Left Uterus. VIII.	No. of Missing Young. IX.	Right. X.	Left. XI.
1	36·4	27·5	8·6	36·1	0·3	5	2	3	0	0	0
6	40·3	25·5	11·7	37·2	3·1	9	3	7	1	4	5
7	39·9	29·4	6·1	35·5	4·4	4	2	3	1	4	0
14	38·4	27·0	9·8	36·8	1·6	7	4	3	0	5	6
20*a*	..	..	..	..	..	11	4	7	0	4	6
24*a*	39·9	25·0	12·0	37·0	2·9	9	5	4	0	5	4
17*a*	39·0	..	..	..	..	8	6	2	0	3	5
18*b*	40·0	..	..	..	..	9	3	6	0	6	3
26*b*	40·5	25·9	11·7	37·6	2·9	9	5	3	+1	?	4
26*c*	36·4	23·4	13·1	36·5	+0·1	10	4	6	0	6	2
21*c*	39·9	27·2	12·5	39·7	0·2	9	6	3	0	4	6
11	40·4	28·0	9·5	37·5	2·9	8	4	6	2	0	0
27*b*	35·0	22·2	10·8	33·0	2·0	9	5	4	0	4	3
25*c*	41·7	26·0	13·3	39·3	2·4	12	5	7	0	4	4
21*b*	..	20·7	19·4	30·1	..	7	5	2	0	4	5
25*a*	35·0	24·7	10·0	34·7	0·3	8	7	1	0	4	5
47*d*	34·7	25·7	8·5	34·2	0·5	7	4	3	0	2	6
							74	70	−4, +1	59	64

IV does not indicate this. According to the size of the litter, the weight of a single young falls on an average from 1⅔ g. in litters of 5 to about 1 g. in litters of 12.

It seemed to me of special interest to compare the number of young of a litter with the number of ova expelled during ovulation which follows immediately after parturition. For an exact comparison the data in columns X and XI require a certain correction, for in 2 mice no eggs were found. Both these ♀♀ had just borne two successive litters; in such cases the ovulation after the second parturition, according to my experience, is generally missed, which seems to be a kind of self-protecting mechanism. Besides, in mouse 26*b* the eggs of one side could not be detected on examination. If to the sum of columns X and XI is added 21, which is about equal to the number of eggs of 2½ ovulations which would have existed normally, the resulting sum corresponds with that of the columns VII and VIII. From this it follows that the number of eggs in the 2 ovulations separated from one another by a period of pregnancy is about equal. Table II shows that no significant losses are caused in the 2nd litter if the 2 ovulations follow each other. In this case the total number of young of the 1st litter is even lower than that of the 2nd, and also the 2 litters follow one another immediately. Larger losses are therefore not probable, though they might have been expected if the ♀♀ after becoming pregnant again had had to nurse the young of the 1st litter.

Another result of the table must be noted. If we compare the distribution of implantations in the 2 uterine horns with the distribution of eggs in the right and left oviduct, we may observe that if, for instance, more embryos have developed in the right horn than in the left, this will be compensated for at the following ovulation, as now more eggs will be expelled on the left side than on the right. From this it follows that (1) the process of maturation in the 2 ovaries is regulated by a higher centre, and (2) the 2 ovaries produce during their activity about an equal number of eggs.

Since these investigations had to be carried out without help, the number of corpora lutea could not be determined. Consequently, in the following figures the mortality of young during gestation is not taken into account. In my records, extending over 2½ years, 504 litters with 3560 young have been recorded. The average litter size is 7·0, a figure which may be looked upon as favourable in comparison with the records of other authors. If we omit the results of the first 6 months, during which my stocks were not yet in good condition, we find an average litter size of 7·15. By selecting only those ♀♀ whose litters were all known to me, the total number of young was 2244, and the average litter size 7·35. The average litter size for all ♀♀ with the same number of litters between the 1st and 7th litter was always between 7 and 7·5. The most frequent litter size was 8, observed 108 times; 93 litters contained 7 young; litters with 11 young were observed nine times, those with 12 four times, and with 13, which is the maximum, once only. The size of the litters varied in the different months from January to June between 7·1 and 7·5, rising to 7·8 in June and reaching the peak in August with 8·3. From then there was a falling-off, the lowest level being 5·6 in November; in December there was a renewed increase with 6·2, while in November and December the average was below 7.

D. DISCUSSION AND SUMMARY.

Several workers have investigated the duration of the sexual cycle in the albino mouse, and their results may be divided into two groups. Some authors, *e.g.* E. Allen (1922) and Parkes (1926, 1928), have found cycles of 4–6 days' duration. In the present investigations also regular cycles lasting 4–5 days have been observed during most months of the year. Only 7 out of 90 ♀♀ failed to become fertilised during the 4 days when they were placed together with the ♂♂, which gives a fertilisation rate of over 92 per cent., as compared with 80·8 per cent. recorded by Parkes (1926) in 88 ♀♀, and 80–90 per cent. recorded by Mirskaia and Crew (1930). The other group of workers consider the normal duration of the cycle to be 9 days. Clauberg states that in the majority of cases he found cornified cells in the vaginal smears only at intervals of 9–10 days, and considers the shorter cycles to be incomplete. This view is shared by Tietze, who thinks that the short cycles are abnormal, and may be due to external agencies. According to Lewis and Wright (1935) the sexual cycle of the mouse varies between 4 and 17 days, and œstrus therefore recurs on an average every 9 days.

These statements show, therefore, that there exist stocks of mice in which the œstrous cycle appears as a rule every 4–5 days, and others in which the time is 9–10 days; these differences must depend on genetical reasons.

In one respect my observations cannot be compared with those of other workers, namely, I did not diagnose œstrum with the aid of the vaginal smears but by the ensuing fertilisation. The low percentage of ♀♀ which are not fertilised within 4 days seems to show that the presence of the ♂ prevents a prolongation of the œstrous cycle; indeed, the characteristic duration of cycle of the race in question can be established only in this way. In the case of ♀♀ which are kept isolated for a longer time, a prolonged cycle must therefore be regarded as the consequence of an abnormal condition. It will be well to observe in the future this point as well as the appearance of cornified cells in the vaginal smear. In a certain opposition to this view is the statement of Parkes (1927), who says that œstrus is delayed when the ♀♀ are kept continuously with a ♂. An atresia of all ripening eggs happened in only a small percentage of the ♀♀ of my stocks.

Three different methods have been used in order to predict the time of birth with a fair degree of accuracy. (1) The presence of the vaginal plug. The ♀♀ should be examined for this twice daily during the first 4 days after mating. In 75 per cent. of cases parturition occurred in the course of the 19th day counting from the time when the plug was found. In the majority of other cases it fell on the 20th day, and only in a few it took place before the 19th day. (2) As the ♀ begins to increase in size, blood will be found in the vagina; this "placental sign" was first observed in the mouse by Parkes (1926). In the present material it was observed between the 11th and the 13th day of pregnancy, from which it follows that the day of parturition may be predicted within a limit of 1–2 days. Busse, who has examined the changes in the ♀ genital tract during pregnancy, does not mention it at all. (3) Finally, the characteristic course of the weight curve during pregnancy has been used to disclose the exact state in which the mouse happens to be. Within the first days of pregnancy the ♀ has a weight increase of only 1–2 g., from the 9th–12th day, of 3–5 g.; the greatest period of growth is the 13th–18th day, when the daily gain in weight may surpass 2 g. On the last day the weight increase ceases, as is also stated to be the case for rabbits (Rosahn and Green). Cooley and Slonaker found that in rats, in which pregnancy lasts on an average 22 days, a sudden rise of weight begins from the 15th day.

With the help of the recording balance, constructed after the principle of a letter-scale and connected with a kymograph with a 24-hour rotation, I succeeded in determining the hour of parturition fairly accurately. The approach of parturition is indicated by the "birth pause," which has an average duration of 4⅔ hr. Parturition begins ½–1 hr. after the beginning of the pause. Besides, the ascents of the scale before and after the pause differ in height. The apparatus is a much simpler construction than that used by Long and Mark, who used a common balance for their birth-recording apparatus and were able to state the approximate time of birth from the different marks of 2 pointers before and after birth. With my apparatus the registration of 1 pointer was sufficient. Long and Mark, who state that they used mice of very mixed ancestry, found that the number of births during the time between 2–6 a.m. is double that at other times. I was able to establish a maximum between midnight and 4 a.m., and a second maximum between 4 and 8 p.m.; fewest births took place in the time from 4 a.m. to 4 p.m.

A comparison between the size of the litter and the number of eggs at the ovulation following parturition showed that both numbers were nearly the same. As, besides, no regression of the average litter size could be established in 2 litters immediately following each other, which is in accordance with the statement of MacDowell and Lord, it may be concluded that in my stocks the number of dead embryos before birth must have been relatively small. This may also be seen from the following: the average litter size of 504 litters observed in 2½ yr. was 7·0 (Copeman and Parsons found 6·7 and Parkes 6·34). MacDowell and Lord, who ascertained by an operative method the number of corpora lutea in the highly pregnant ♀♀ and compared them with the number of young, found that 39·9 per cent. of the eggs which matured failed to give rise to young. By direct observation I established in 17 ♀♀ that the percentage of young eaten during parturition was only 2·5, as demonstrated by a comparison of the number of the still bloody implantations in the uterus with the number of young. The average litter size, calculated for the different months, reached a maximum in August with 8·3 and a minimum in November with 5·6.

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VIII.—Factors affecting the Hatching Weight of Brown Leghorn Chickens.

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INTRODUCTION.

ROUTINE observations on the growth of chickens from a flock of Brown Leghorns maintained at this Institute indicated that factors, apparently closely associated with season of the year, caused considerable variations in the rate of growth. It is possible to conceive of two distinct means by which seasonal factors may produce their effect (1) directly on the growing chick, or (2) indirectly in that their influence may be exerted on the hen and transmitted to the egg from which the chick subsequently develops; either or both may contribute to the final variations obtained.

It is to the second postulation that attention has been directed in this communication. Since the egg, artificially incubated, develops under conditions which are relatively constant, variations in embryonic growth-rate may be taken as being mainly referable to factors inherent in the egg. After hatching this is no longer true. Hatching weight has been used, therefore, as an index of rate of chick growth for the particular phase of the general problem under consideration.

From observations made during the usual hatching season (spring) Upp (1928) had noted that the correlation between hatching weight and egg weight varied from period to period. In the present study similar data derived from the Institute stock for the complete year are examined, together with some further records, which, it was hoped, might provide a reasonable explanation of the varying dependence of hatching weight of chick on egg weight throughout the different seasons.

MATERIAL.

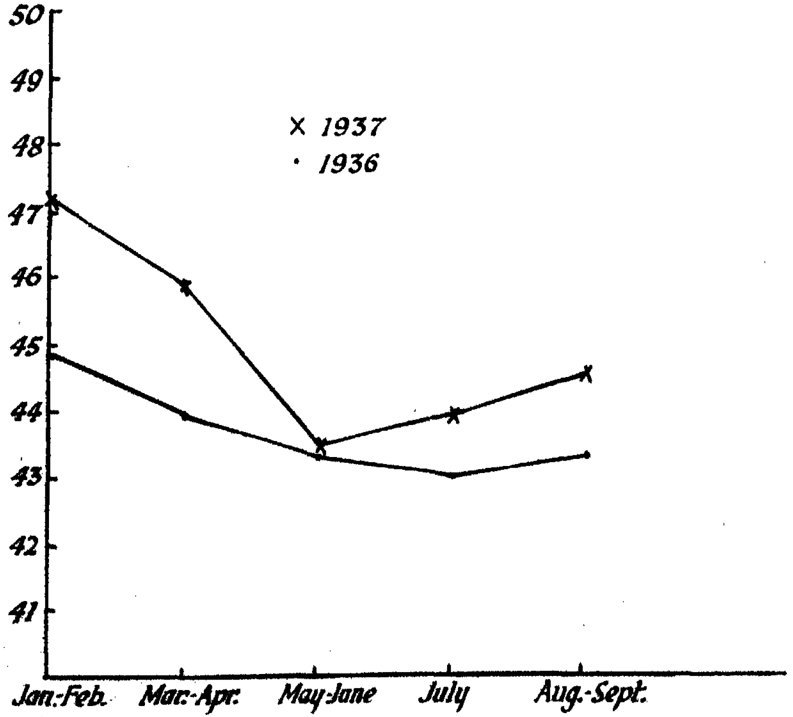
The data presented were collected in 1936 and 1937. The 1937 records were from a planned experiment designed to show that the seasonal changes in hatching weight indicated by the earlier observations were significant. Those of 1936 were collected by routine observation, and could not be considered as critical as the later data.

For the planned experiment a pen of thirteen 2- and 3-year-old birds, selected for their previous records of good hatchability and fertility, were mated to one male, and kept in the same pen throughout the year. Every egg laid was weighed and incubated; all the chickens were pedigreed. The environment was kept as nearly constant as possible, the incubator—an electric Petersime—being housed in a warm room where temperature fluctuations certainly occurred, but were considerably less than those of the external atmosphere.

The 1937 data have been presented as the critical data, other figures have been included to demonstrate the similarity of the trends for growth behaviour from year to year.

RESULTS.

Preliminary analysis of data collected during 1936 had indicated that hatching weight decreased from the time of onset of reproductive activity till the summer, and then increased in the autumn. Table I, with Graph I, shows the seasonal change in hatching weight in 1936 and 1937. The 1936 data were from a discontinuously changing parent population, the



GRAPH I.—Showing the seasonal hatching weight in 1936 and 1937.

1937 from the planned experiment. It will be seen that hatching weight declines from the time of onset of egg production to be minimum in the summer months and then increases slightly in the autumn. Chickens have been referred to the month in which the egg was laid and not to the month of hatching.

TABLE I.—THE SEASONAL CHANGES IN HATCHING WEIGHT IN 1936 AND 1937.

Season.	No. of Chicks.	Hatch Wt., 1936. In g.	No. of Chicks.	Hatch Wt., 1937. In g.
January–February	300	44·86 ± ·193	133	47·20 ± ·280
March–April	566	43·98 ± ·156	239	45·92 ± ·252
		Drop significant.		Drop significant.
May–June	271	43·41 ± ·194	225	43·47 ± ·249
		Drop significant.		Drop significant.
July	148	43·08 ± ·190	143	44·00 ± ·262
August–September	202	43·36 ± ·223	229	44·64 ± ·221
				Rise significant.

EGG WEIGHT AND EGG NUMBERS.

Upp (1928) showed that the hatching weight of chickens was correlated with egg weight, and, further, he found that the correlation coefficient r varied from period to period. His observations were restricted to the spring hatching season—late December to early May.

Jull (1924) reported, for yearling birds, a gradual rise in egg weight from the time of onset of egg production till February, followed by a considerable drop from February to May. From May to September egg weight remained fairly constant, rising, however, in October and November. Further, he has shown that egg numbers increased from the time of onset of egg production to attain a maximum in the spring months, after which they slowly declined till the moult caused a cessation of reproductive activity

From Table II and Graph II it will be seen that our 2- and 3-year-old birds obeyed the same general rule as did his yearling hens. The seasonal differences shown in egg weight were significant. The 1937 curve differed somewhat from the 1936 one but the general trend was the same, suggesting that there is a typical annual curve which varies only in minor details from year to year.

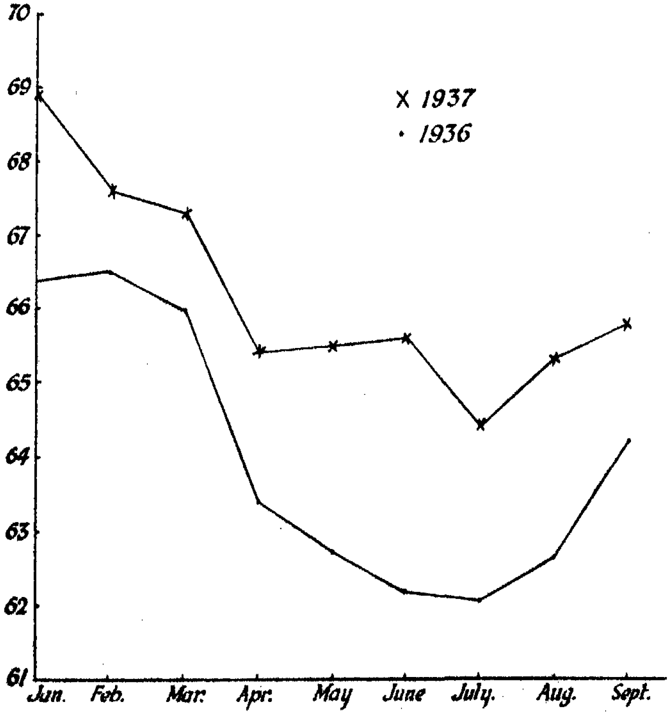
Graph III, for egg numbers, showed that the decrease in egg weight was accompanied by a simultaneous increase in egg numbers. Egg production attained its maximum, and began to decrease prior to the termination of the decline in egg weight. From June to September inclusive, egg numbers gradually declined. The two most obvious interpretations suggested for the continued fall in egg weight after production was declining were (1) that the hen required a certain length of

TABLE II.—THE CHANGE IN MEAN EGG WEIGHT TOGETHER WITH THE CHANGE IN THE AVERAGE NUMBER OF EGGS PER MONTH AS THE LAYING YEAR PROCEEDS.

Months.	1937.		1936.	
	Aver. Egg No. per Bird.	Mean Egg Wt. in g.	Aver. Egg. No. per Bird.	Mean Egg Wt. in g.
January	6·7	68·93 ± ·404	9·3	66·39 ± ·388
February	12·7	67·56 ± ·248	13·3	66·46 ± ·269
March	18·3	67·29 ± ·244	20·8	65·50 ± ·259
April	18·6	65·40 ± ·261	21·2	63·24 ± ·253
May	18·7	65·51 ± ·239	20·6	62·73 ± ·274
June	17·3	65·55 ± ·272	18·8	62·23 ± ·296
July	16·1	64·38 ± ·312	19·4	62·03 ± ·294
August	15·9	65·27 ± ·327	16·8	62·64 ± ·339
September	15·7	65·83 ± ·365	15·9	64·20 ± ·390

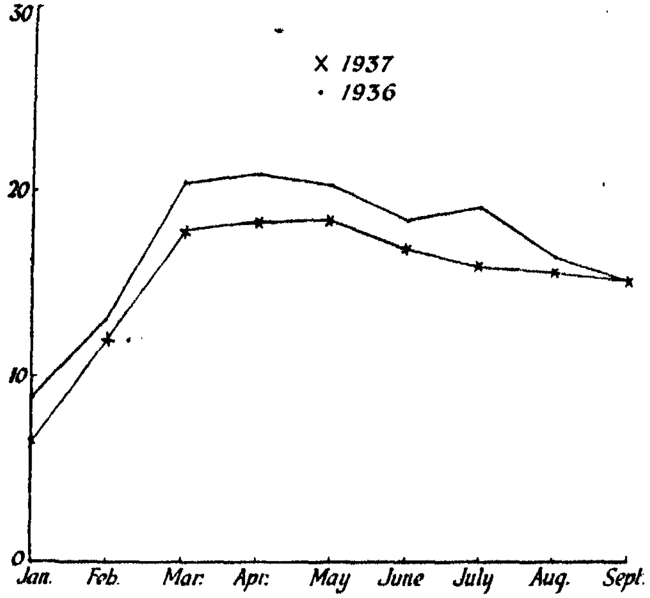
The 1936 data were from a group, chosen at random, of twenty 2-year-old birds commencing to lay in January; the 1937 figures were from the thirteen birds used in the planned experiment.

time to recover from the drain of high reproductive activity, or (2) that a summer metabolic rate due to physiological factors was antagonistic to both high egg production and high egg weight. If the latter suggestion were correct it would imply that the egg weight was not dependent upon



GRAPH II.—Showing the monthly variation in egg weight in the years 1936 and 1937.

egg number, but that both were controlled by a third factor, possibly endocrine in nature; it will be suggested later that the thyroid gland may influence egg weight.



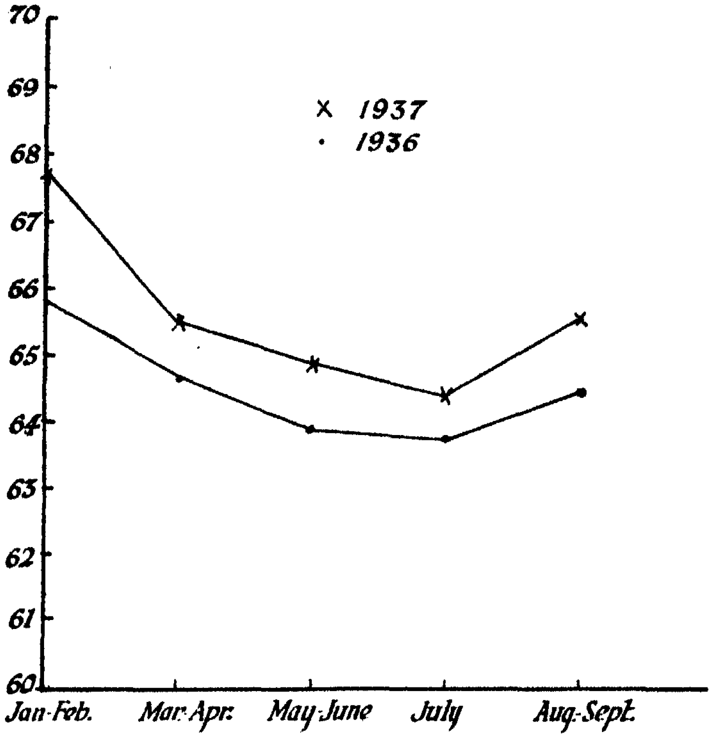
Graph III.—To show the monthly variation in egg numbers in 1936 and 1937.

Table II and Graph II show the change in the egg weight for all eggs laid; Table III and Graph IV show the seasonal change in egg weight in 1936 and 1937 for the eggs that hatched. The population was the same as that for Table I; the figures of Tables I and IV being directly comparable.

TABLE III.—THE SEASONAL CHANGE IN THE WEIGHT OF EGGS THAT HATCHED IN 1936 AND 1937.

Season.	No. of Chicks.	Egg Wt., 1936. In g.	No. of Chicks.	Egg Wt., 1937. In g.
January–February	300	65·80 ± ·127	133	67·72 ± ·343
March–April	566	64·67 ± ·182	239	65·52 ± ·300
		Significant drop.		Significant drop.
May–June	271	63·91 ± ·228	225	64·88 ± ·273
		Significant drop.		Significant drop.
July	148	63·80 ± ·229	143	64·40 ± ·346
August–September	202	64·45 ± ·253	229	65·63 ± ·282
		Significant rise.		Significant rise.

Upp (1928) has been mentioned as showing that a change in the correlation coefficient, r, for hatching weight and egg weight, took place as the hatching season proceeded. Correlation coefficients for the 1936 and 1937 seasons showed that the dependence of hatching weight on



GRAPH IV.—Showing the seasonal variation in the weight of eggs that hatched in 1936 and 1937.

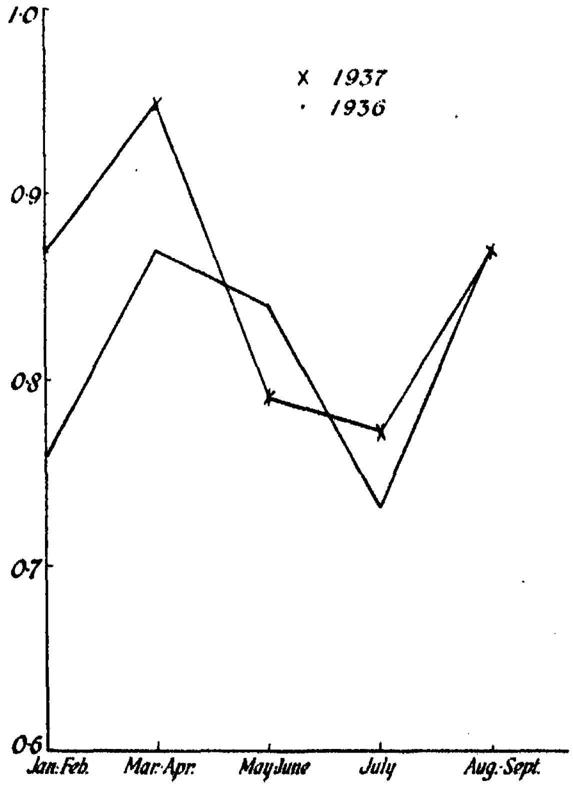
TABLE IV.—SHOWING THE SIGNIFICANCE OF THE CHANGES IN CORRELATION COEFFICIENT r FOR HATCHING WEIGHT ON EGG WEIGHT FROM SEASON TO SEASON IN 1937.

Season.	r.	z.	Difference in z.	$n-3$.	Reciprocal.
January–February	+·87	1·34		130	·00769
March–April	+·95	1·84		236	·00424
			·50 ± ·109		·01193
					Significant.
March–April	+·95	1·84		236	·00424
May–June	+·79	1·07		222	·00451
			·77 ± ·093		·00875
					Significant.
May–June	+·79	1·07		222	·00451
July	+·77	1·02		140	·00714
			·05 ± ·108		·01165
					Not significant.
July	+·77	1·02		140	·00714
August–September	+·87	1·34		225	·00444
			·32 ± ·107		·01158
					Significant.

P was less than ·01 for all values of r (Fisher, 1936, pp. 206–213).

egg weight was always high, never less than ·76, but nevertheless the dependence varied from season to season. The groupings used were January and February, March and April, May and June, July, and August and September.

From Tables IV and V with Graph V it will be observed that dependence in both 1936 and 1937 increased significantly from the January–February period to the March–April one. From March–April to July there was a significant decline in the values of the correlation coefficient, the value of r being least in July. The 1936 May–June drop was not significant. This may be accounted for by the fact that in 1936 in the March–April period many of the eggs incubated were from experimental stock which never developed very vigorous embryos; hence the dependence was lowered in this period. Secondly, from May onwards eggs were incubated only from birds giving good hatchability and fertility and



GRAPH V.—Showing the seasonal changes in the value of the correlation coefficient r for hatching weight with egg weight in 1936 and 1937.

TABLE V.—TO SHOW THE CHANGES IN THE CORRELATION COEFFICIENT r FOR HATCHING WEIGHT ON EGG WEIGHT DURING THE YEAR 1936. THE CHICKENS IN ANY ONE PERIOD WERE NOT NECESSARILY FROM THE SAME PARENTS AS THOSE IN ANY OTHER PERIOD.

Season.	r.	z.	Difference.	$n-3$.	Reciprocal.
January–February	+·76	1·01		297	·00337
March–April	+·87	1·34		563	·00178
			·33 ± ·072		·00515
					Significant.
March–April	+·87	1·34		563	·00178
May–June	+·84	1·22		268	·00373
			·12 ± ·074		·00551
					Not significant.
May–June	+·84	1·22		268	·00373
July	+·73	·93		145	·00690
			·29 ± ·103		·01063
					Significant.
July	+·73	·93		145	·00690
August–September	+·87	1·34		199	·00503
			·41 ± ·109		·01193
					Significant.

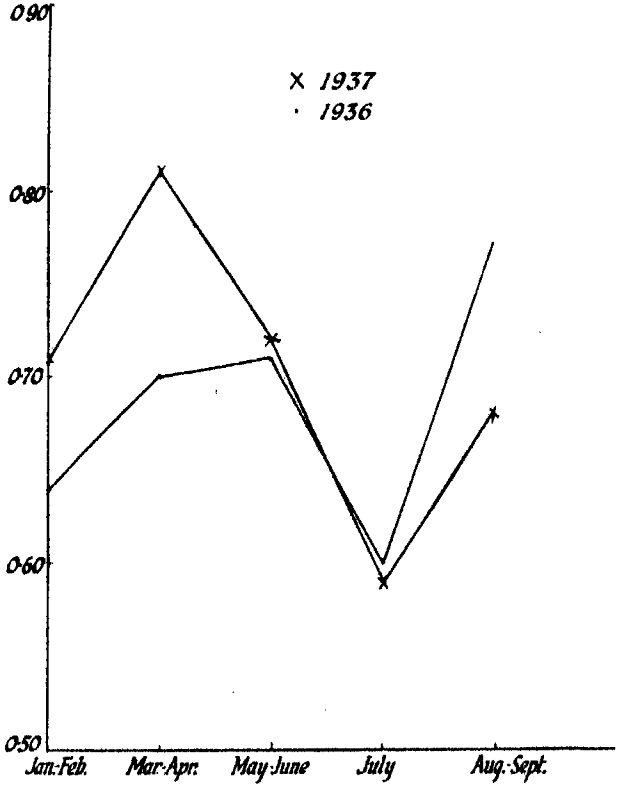
P for r was always less than ·01 (Fisher, 1936).

within a certain range of egg weight; therefore the comparison was between chickens from a selected group of birds and those from an unselected group. The 1937 data, on the other hand, was from the same parent stock throughout the year, and all the eggs from that stock were incubated, therefore each season was directly comparable with any other season. Another factor influencing the 1936 data was that from May onwards the eggs of pullets were gradually replacing the eggs of older birds, so that not only the individuals, but the age of the parent population, was changing discontinuously. From this it will be seen that the 1937 data were the more critical, and therefore the May–June drop occurring in this year must be considered more nearly correct than the non-significant drop in the corresponding period in 1936.

In the August–September period the dependence increased, returning in 1937 to the same level as in the January–February period. In 1936 the August–September level of dependence was higher than its January–February period. The same explanations that accounted for the discrepancies in the March–April and May–June periods apply to the January–February and the August–September periods.

It can now be concluded that the general trend of the dependence of hatching weight on egg weight varied as the laying year proceeded, the dependence being greatest in the March–April period and least in the July one.

The value of r has been shown to change with the season, and the nature of the change can best be demonstrated by reference to the changes in the regression coefficient *b*, for hatching weight on egg weight. The weight of both is in grams, so that an increase of 1 g. in egg weight results in an increase in hatching weight varying from ·59 to ·81 g



GRAPH VI.—Showing the seasonal variation in the regression coefficient *b* for hatching weight on egg weight in 1936 and 1937.

Graph VI, with accompanying Tables VI and VII, demonstrates that changes in the value of *r* were accompanied by corresponding changes in the value of the regression coefficients. The 1937 curves for both the regression and the correlation coefficients follow the same trend. The 1936 non-significant May–June drop in the value of *r* was countered by a non-significant May–June rise in the regression coefficient.

From the regression coefficients it was apparent that the variation in dependence was due to the extent of the ability of the developing embryo to utilise the egg substance provided; this ability was greatest in the March–April period and least in the July one.

TABLE VI.—THE CHANGE IN REGRESSION COEFFICIENTS *b* WHEN THE DATA WERE FROM THE SAME PARENT STOCK—1937 DATA.

Season.	*b.*	Difference.		*t.*		
January–February	·71					
March–April	·81					
		$b_2 - b_1$	·10	3·0211	*t* for P ·01	2·57582
			Highly significant.			
March–April	·81					
May–June	·72					
		$b_1 - b_2$	·09	2·3872	*t* for P ·01	2·57582
					t for P ·02	2·32634
			Significant.			
May–June	·72					
July	·59					
		$b_1 - b_2$	·13	2·4648	*t* for P ·01	2·57582
					t for P ·02	2·32634
			Significant.			
July	·59					
August–September	·68					
		$b_2 - b_1$	·09	1·9607	*t* for P ·02	2·32634
					t for P ·05	1·95996
			Just significant.			

The method used for comparing the regression coefficients was that given by Fisher (1936, pp. 146–148).

TABLE VII.—TO SHOW THE CHANGE IN REGRESSION COEFFICIENTS WHEN THE DATA ANALYSED WERE FROM A DIFFERENT PARENT POPULATION IN THE DIFFERENT SEASONS—1936 DATA.

Season.	*b.*	Difference.		*t.*		
January–February	·64					
March–April	·70					
		$b_2 - b_1$	·06	2·2727	P ·05	1·95996
					P ·02	2·32634
						Significant.
March–April	·70					
May–June	·71					
		$b_2 - b_1$	·01	·34602	P ·7	·38532
					P ·6	·52440
						Not significant.
May–June	·71					
July	·60					
		$b_1 - b_2$	·11	1·89328	P ·1	1·64485
					P ·05	1·95996
						Just significant.
July	·60					
August–September	·77					
		$b_2 - b_1$	·17	3·23809	P ·01	2·57582
					P ·05	1·95996
						Highly significant.

(Fisher, 1936, pp. 146–148.)

From the evidence presented it is seen that the following facts have been elucidated:—

(1) The curve for hatching weight over the laying year declined and then inclined, the lowest weight occurring in the summer months.

(2) Correlation coefficients evinced that hatching weight was dependent on egg weight, but that the dependence varied from season to season.

(3) Regression coefficients indicated that the changes in the dependence were due to the fact that in the summer months the increase in hatching weight for an increase in egg weight was not of the same magnitude as the increase for a corresponding egg-weight rise in the spring months.

(4) Egg weight decreased from the time of onset of egg production till the end of the summer—July—and then increased till the moult terminated reproductive activity in the autumn.

(5) Egg numbers increased during the first part of the laying year, maximum production occurring in the late spring, after which they slowly declined till the moult.

Reviewing these facts it would appear that, on the whole, increased reproductive activity leads to a diminution of the egg size and, therefore, to a decrease in hatching weight. It is undoubtedly correct that decreased egg size accounted for a considerable proportion of the decrease in hatching weight, but it does not account for the change in dependence nor for the varying ability of the embryo to utilise the nutriment provided in the egg. Further, the continuation of the decline in egg weight after egg production had begun to fall, seen in both years, cannot be regarded as entirely due to the prolonged effect of high egg production, for during the period of highest reproductive activity, in March and April, the regression coefficient was greater than in any other month. If the number of eggs produced lowered the egg quality so that the developing embryo was gradually receiving less of the necessary nutriment, one would expect that the highest value of b would occur in January and February.

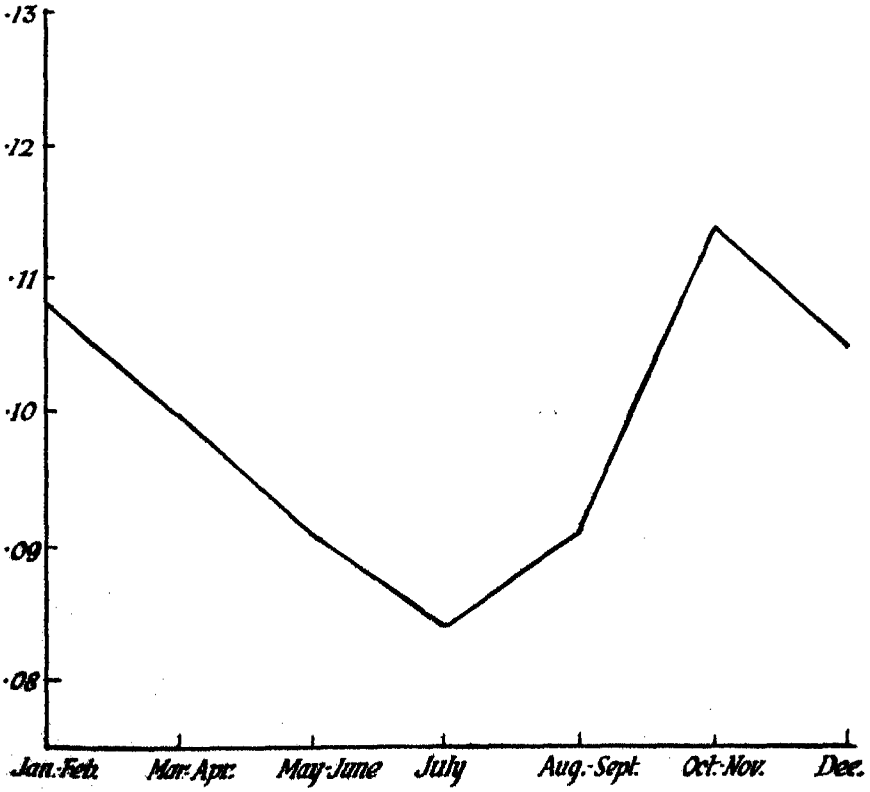
Thus, it was imperative to look for some physiological factor affecting the metabolism of the hen in such a way that it might have an antagonistic effect upon egg production and egg weight, together with an inhibiting effect upon embryonic growth.

Analysis of data on thyroid weights collected at the Institute of Animal Genetics revealed that thyroid weight decreased from the time of onset of laying until July and then increased, attaining maximum weight in October and November when the moult occurred (see Table VIII and Graph VII). An interesting point was the increase in July thyroid weight, when moulting birds were included with the laying ones; this indicated that thyroid size was in some way connected with the physiology of the moult.

TABLE VIII.—THE SEASONAL CHANGES IN THYROID WEIGHT.

Season.	No. of Individuals.	Thyroid Wt. In g.	Difference.
January–February .	42	·1084 ± ·0045	
			·0084 just significant.
March–April . .	42	·1000 ± ·0042	
			·0088 significant.
May–June . .	95	·0912 ± ·0034	
			·0072 significant.
July . . .	9	·0840 ± ·0021	
			·0073 significant.
August–September	62	·0913 ± ·0028	
			·0235 significant.
October–November	124	·1148 ± ·0021	
			·0100 significant.
December . .	45	·1048 ± ·0043	

July thyroid weights have been given for laying birds only; inclusion of 9 moulting birds increased the thyroid weight from ·0840 ± ·0021 to ·1047 ± ·0094, and the number to 18 birds.



GRAPH VII.—Showing the seasonal change in thyroid weight.

DISCUSSION.

Hatching weight has been shown to be dependent on egg weight, but the particular interest of this study lies in the manner and extent to which the dependence varies with the season. Apart from the initial period covered by the observations, the relationship varies in orderly fashion, the dependence being greatest in the March–April period and least in July. (Perhaps it is to be expected that at the onset of the reproductive cycle, physiological forces of a complex nature will be involved which subsequently will not be reproduced; therefore, it may be expected that, at this period, an atypical behaviour will be induced.)

In an attempt to elucidate the causes underlying the phenomenon described, it first of all may be suggested that the seasonal changes in egg weight are a reflection of a relatively orderly change, throughout the year, in the metabolic level of the hen, *i.e.* large eggs are produced during the periods of lowered maternal metabolism, but when the intensity of reproductive function increases (as shown by increase in the rate of egg production) coincidentally the eggs become smaller. On this assumption the metabolic rate of the hen increases to a maximum in July.

Riddle and Fisher (1925), from their studies on the pigeon, suggested that the metabolic rate of the parent was inherent in the egg and transmitted to the developing embryo. This leads to the problem of the respective levels of metabolic functioning involved in the two distinct processes of egg and chick formation. It may be expected that they would be governed by the same rules. While the correlation figures bear out this assumption, the regularity of the regression-coefficient curve suggests the presence of some additional differential factor at work in their developmental processes in order to account for the observed variation in the ratio of their completed masses.

The egg can take no part in the process of its own formation, and it has been shown that the greater part of its bulk is laid down in a comparatively short time (Riddle, 1916). On the other hand, the chick embryo takes three weeks to attain hatching weight; during that time its own endocrine system develops, and must be assumed to play some rôle in the later stages of embryogeny.

Whether the forces hitherto controlling developmental processes are gradually replaced by those derived from the embryo, or whether pre-embryonic and embryonic factors continue to work together until hatching, producing a synergistic effect, is unknown, but if the latter were true, it would suggest an explanation of the varying discrepancy between egg weight and chick weight at hatching.

Greenwood and Chaudhuri (1928), from a study of the effects of thyroxin injections to incubating eggs, attributed the production of dwarf embryos to an increased metabolic rate. If, as is suggested from this work, the active secretion of the thyroid gland may be considered a major factor in determining growth-rates in chicken embryos, then it might be suggested that seasonal changes in chick weight were a reflection of varying levels of thyroid activity in the hen, the effects being intensified if, at the same time, a change in the embryonic growth-rate affects the functioning of the embryonic endocrine system.

From an analysis of data collected at the Institute on the variation in thyroid weight with season, it was found (Graph VII) that the curve for gland weight followed the same trend as that for egg weight. This means that if thyroid weight were to be taken as an indication of function, then at the time of postulated highest metabolic rate in the embryo (July) its function was inversely related to its mass. That the thyroid gland of the fowl possessed the greatest amount of colloid in the winter-time (Podhradsky, 1933) suggests that at this time the gland was acting as a storage agent for its secretion. If this were so, then the decrease in amount of stored colloid at other periods of the year might be attributed, not to a decreased level of secretion, but to an increased level of excretion.

The investigations of Riddle *et alii* on thyroid-gland size in pigeons have led to the conclusion that, as in the fowl, the season of active reproduction covers the period of decline in thyroid size.

Riddle (1927) attributes these changes to responses to external temperature variations, but the data given in Table VIII, indicating the significant difference between thyroid weights of laying and non-laying hens in July, strongly suggests an inverse relationship between thyroid size and reproductive activity in the fowl, irrespective of any dependence on temperature variation. The solution of the problem requires a more accurate measurement of thyroid function than is available at the present time.

Finally, it must be emphasised that the seasonal behaviour evinced must be modified to suit the individual laying cycle of any bird or group of birds that does not conform to the laying cycle for the birds used in this experiment; the trend demonstrated was for yearling birds whose second laying year began in January.

SUMMARY.

1. It has been shown that seasonal changes in the embryonic growth-rate of chickens occurred.

2. Egg numbers increase in the first half of the laying year, and decrease from May till the onset of the moult causes a cessation of reproductive activity.

3. Hatching and egg weight decline while egg numbers increase, and increase after the rate of egg production decreases.

4. The dependence of a hatching weight on egg weight, as evinced by correlation coefficients, increases from the January–February period to the March–April one, decreases till July, and increases in the autumn.

5. Regression coefficients reveal that the change in dependence is due to the varying ability of the embryo to utilise the egg substance provided. The trend of the curves for regression and correlation coefficients was similar.

6. Thyroid weight decreases from the time of onset of reproductive activity till July and then increases, attaining maximum weight in October and November, *i.e.* during the moulting period.

7. The seasonal changes in the dependence of hatching weight on egg weight have been interpreted as the expression of a varying maternal metabolism, the changes in the metabolic rate being related to thyroid activity.

ACKNOWLEDGMENT.

The writer wishes to acknowledge her indebtedness to Dr A. W. Greenwood and Dr J. S. S. Blyth for their co-operation and constructive criticism.

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IX.—Gynandromorphism and Lateral Asymmetry in Birds.

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(With One Coloured Plate.)

(MS. received December 14, 1937. Revised MS. received March 3, 1938. Read November 8, 1937.)

SHORTLY after Juhn, Faulkner and Gustavson (1931) had shown that natural differentials in the growth-rate of individual feathers on one and the same fowl determined, in part, the threshold of their response to œstrin, the faster the growth-rate the greater being the amount of œstrin required to produce female feathering, Lillie (1931) extended their conclusions to a re-examination of the cases of lateral gynandromorphism in birds recorded in the literature up to that time. He pointed out that this condition seemed always to be associated with lateral size asymmetry, and argued therefore that, since the male side was the larger and presumably the faster growing, to account for lateral gynandromorphism it was necessary only to postulate that the ovary of the bird should be malfunctioning, producing a sub-normal amount of œstrin, sufficient to evoke henny-feathering on the smaller, more slowly growing side, but insufficient to do so on the larger, faster growing side.

This brilliant suggestion found support in the fact that all the lateral gynandromorphs reported had shown themselves to be either infecund or else irregular layers. Furthermore, the deficiency of œstrin, demanded by this hypothesis, in those birds which possessed testicular as well as ovarian tissue was readily explained by an appeal to the gonad-pituitary relationship that had been demonstrated by the work of Leonard, Meyer and Hisaw (1931), Moore (1931), Moore and Price (1932) and Greenwood and Blyth (1930).

Lillie did not consider the cause of the lateral size asymmetry or of the dual nature of the gonads; he was concerned solely with the presentation of the argument that, given a malfunctioning ovary and lateral size asymmetry with different rates of feather growth on the two sides of the body, all cases of lateral gynandromorphism in birds could be explained by reference to the facts disclosed by his co-workers. He did not discuss, therefore, the possibility that an aberrant chromosome distribution, such as that shown by Morgan and Bridges (1919) to underlie gynandromorphism in Drosophila, might itself be the cause of the lateral size asymmetry, and thus be responsible indirectly for the lateral differences in plumage characterisation.

Since that time a number of additional facts have been disclosed which show that Lillie's explanation cannot be of general application. The work of Keck (1934) on the house-sparrow, of Danforth and Price (1935) on the blackbird and of Danforth (1937 *a*) on the pheasant has made it clear that among birds there is considerable variation in the degree to which feather-type is dependent upon humoral influences. Apparently there are two main types—the *sparrow-type*, in which the plumage characters are determined predominantly by genetic factors and in which the feathers are not noticeably affected either by castration or by hormone injection; and the *fowl-type*, in which the plumage characters are predominantly determined by hormonal factors and in which the agonadic bird exhibits male-type plumage, while œstrin induces henny-feathering. There is, in addition, a third type, the *pheasant-type*, in which the imposition of one sex-hormone upon the contra-sex genotype evokes an intersexual plumage (Danforth, 1937 *a* and *b*).

All the clear-cut cases of lateral gynandromorphism so far reported have occurred in two closely related species, the chaffinch (*Fringilla cœlebs*) and the bullfinch (*Pyrrhula europæa*). It is known that the lateral plumage gynandromorphic finch can continue, moult after moult, simultaneously to regenerate male-type feathering on one side of the body and female-type feathering on the other. In the case of the fowl, in which form gynandromorphs have been described by Macklin (1923), Vecchi (1936) and Hutt (1937), it is established that in the normal bird there are considerable and appreciable differences in the growth-gradients of regenerating feathers in different skin regions of one and the same bird. So that if Lillie's hypothesis is to be sustained, it is necessary to assume that not only is the degree of ovarian deficiency fixed by chance at a constant and critical level, but also that the most slowly growing region on the larger side of the body grows at a faster rate than does the fastest growing region on the smaller side.

We are fortunate in that we are able to present eight new cases of lateral asymmetry in birds which permit us to suggest that lateral gynandromorphism, like simple lateral size asymmetry, is the result of aberrant distribution of the chromosomes at the first cleavage division, and that there are three types of the condition corresponding to the classification given above: (1) the sparrow-type, in which the plumage characterisation of each side of the body is determined by the genetic constitution of that side; (2) the fowl-type, in which the plumage characterisation of both sides is subject to hormonal regulation; and (3) the pheasant-type, less common, in which a nearly normal sex type of plumage is exhibited by one side of the body, an intersexual type by the other. In the sparrow-type a gynandromorph can be a true "half-sider"; in the fowl-type and the pheasant-type the half-sider in respect of sex-dimorphic plumage characterisation is an impossibility.

In the first four of these new cases the sex-characters are not involved. They are instances of simple lateral asymmetry. The first is a yellow-buff Yorkshire cock canary which was bred in 1935 by Mr J. J. Shepherd of Romford, from whom we obtained it. Mr Shepherd himself accurately described the bird as "a true half-sider, the dividing line between the buff and the yellow sides passing from the vent, along the exact mid-line of the breast, over the middle of the crown and down the centre of the back. The parents of this bird were a clear yellow cock and a clear buff hen, both outstandingly rich in colour. Its brothers and sisters were normal. It was noted that the egg from which this half-sider was hatched (one of a second-round clutch of four) was of abnormal size, being almost twice as large as the ordinary canary egg. The half-sider itself, on hatching, was appreciably larger than the other three chicks. Even its nest feathers were different in colour on the two sides of the body. It is now an excellent exhibition type of Yorkshire cock."

The genetic relationship between yellow and buff is confused, mainly owing to the fact that it is the rule with fanciers never to breed buff to buff or yellow to yellow. Not infrequently a particular bird, when exhibited, wins first as a yellow and later as a buff, or *vice versa*. There are plentiful records in the fanciers' journals of buffs, after a moult, becoming yellows. It is not surprising, therefore, to learn that the mating buff × buff gives both buffs and yellows, and that yellow × yellow yields yellows and buffs.

The bird now being described is yellow on the right side, buff on the left. Mated to a buff hen it has produced five young, but none of these has been successfully reared. There is no reason to ascribe this early post-natal mortality to the asymmetry of the father, for canaries are notoriously difficult to rear. Micrometer measurements of the long bones of this bird show that those on the buff side are on the average 4·3 per cent. smaller than are those of the yellow side.

The second case is that of an Old English Game bantam hen (fowl A). The plumage on the left side was the typical partridge colour, that on the right typically spangled. Spangling in the Old English Game takes the form of a white tip on a black or partridge feather, in contrast with the spangling of the Hamburgh, in which there is a black tip on a silver or white feather. Mated to a spangled Old English Game cock this hen produced both spangled and non-spangled offspring. Unfortunately, before bone measurements were taken, she was killed and eaten by dogs. In order to determine the genetic nature of spangling in the Old English Game bantam the matings shown in Table I were made.

TABLE I.

Mating.	Hen Number.	Offspring Total.	Non-spangled.		Spangled.	
			♂♂	♀♀	♂♂	♀♀
P_1 Spangled ♀♀ × P_1 Black-red ♂	17	23	10	13		
	241	30	12	18		
	334	34	15	19		
	..	87	37	50		
P_1 Partridge ♀♀ × P_1 Spangled ♂	5	18	7	11		
	90	1	1	0		
	221	22	13	9		
	266	15	2	13		
	Unrecorded floor eggs.	36	15	21		
	..	92	38	54		
F_1 Partridge ♀♀ × F_1 Black-red ♂	..	154	48	62	27	17
Backcross. F_1 Partridge ♀♀ × P_1 Spangled ♂	1303	4	3	..	1	
	161	19	4	6	7	2
	..	23	7	6	8	2

It seems clear from these data that spangling in this breed is a monogenic autosomal recessive character and quite unrelated to the Hamburgh spangling, which Taylor (1932) found to be an autosomal dominant.

The third case is that of a cockerel (B), out of the mating Light Sussex hen × Rhode Island Red cock, and thus heterozygous for silver. It was obtained through Professor Punnett from Miss Eldridge of Maysland Farm, Dunmow. The colour of the skin and shank of the right side of the bird is white, that of the skin and shank on the left side yellow. The dividing line follows the mid-line of the body throughout, bisecting the vent and the upper and lower beak. The bird is now eight months old and is still living. Measurements of its long bones reveal a difference of 2·9 per cent. in favour of the right white side.

The fourth case is that of a Light Sussex cockerel (C) bred by Mr Walter Heale of Canterbury, and obtained by us through the mediation of Professor Punnett. It is known that Rhode Island Red blood had been introduced into Mr Heale's flock a few years ago, but that it had been largely bred out, until now all the chicks that are hatched exhibit the typical Light Sussex plumage colours, though a very small percentage still have yellow shanks and skin colour. This bird is very similar to case B; it is white on the right and yellow on the left. When it was first seen by us in May 1937 it was five months old and no appreciable lateral size asymmetry existed, but two months later this had become manifest. The bird was killed in September and its skeleton prepared, when it was found that the bones of the appendicular skeleton on the yellow side were on the average 2 per cent. shorter than those of the right white side. Prior to its death this bird had been mated to recessive yellow-fleshed Brown Leghorn hens. By means of a special technique, involving cloacal entry, the products of each of the testes were collected and used separately in artificial insemination. The male proved to be highly fertile in such matings, and over a period of six weeks 54 chicks were hatched from four hens. Fifty of these were reared to the age of five weeks or beyond, when the leg colour had become clearly distinguishable. Among 17 of these chickens, derived from eggs fertilised by sperm from the left testis, 6 were white and 11 were yellow. Of the 20 derived from sperm from the right testis, 9 were white and 11 were yellow. The remaining 13, originating either from mixed semen or else from unidentified floor eggs, included 9 whites and 4 yellows. Thus there were 24 whites and 26 yellows, both sorts originating from both testes in proportions which did not significantly differ. It is clear that the genetic constitution of the left testis was not identical with that of the left soma; both testes would seem to have been genetically heterozygous (Ww).

The next four cases differ from the preceding in that they are instances of lateral gynandromorphism, the condition in which male characterisation is present on one lateral half of the body, female characterisation on the other, the individual belonging to a species in which the sexes are normally separate and distinct.

Two of these gynandromorphs were found in the Gouldian finch (*Gouldæornis gouldiæ*), a native of Australia, and were discovered among a large importation of Australian birds. The male has a hood of deep velvety black covering the forehead, lores, cheeks, ear-coverts and upper throat. This is encircled posteriorly by a narrow band of cobalt blue which blends into the yellowish green of the back and wings; the neck and anterior breast are a shining lilac purple. The under-surface is a rich yellow. The female is a duller and quieter edition of the male, the lilac and golden yellow of the latter being replaced by pale rose and light yellow.

The two mosaics now being described are hens, their behaviour being in every way that of the normal female; both have mated with males and both have laid eggs. They possess male-type plumage on the right side of the body, female-type on the left (Plate). One of them died, and post-mortem examination revealed a typical ovary and accessory apparatus on the left side of the body; no testicular tissue was anywhere present. The other is still alive, and examination of the reproductive organs has not yet been attempted. Careful examination showed that the average linear difference between the two sides of the bodies of these birds was of the order of 2 per cent., the bones of the right side with the male-type plumage being the larger.

Subcutaneous implantation of œstrin crystals in a normal male Gouldian finch had no effect upon the colour of the subsequently regenerating feathers, these being as lilac as were those they replaced. Similarly, implantation of crystals of testosterone in a normal female failed to produce any male coloration in the regenerating feathers. This experimental procedure was repeated on several occasions and in both sexes, but invariably gave completely negative results in so far as the colour of the feathers was concerned. But it was noticed that, in the case of the normal male, the narrow terminal fringe of the lilac breast feather disappeared under the influence of œstrin, and microscopic examination showed that this alteration in feather structure took the form of an extension of barbules to the ends of the barbs, as is the case in the normal female feather. This modification of structure in no way altered the actual appearance of the breast, but it did serve to show that the dosage of œstrin employed was physiologically effective. Similar-sized crystals of œstrin, when implanted into the fowl, induced henny-feathering in the male, and, as Parkes (1937) has shown, this procedure constitutes a most efficient method of continuous hormone administration. There can be no doubt, therefore, that the amount of hormone supplied to the normal male and female finches in this experiment exceeded the threshold of physiological effectiveness.

It thus became clear that these two finch gynandromorphs belonged to the sparrow-type, in which sex-dimorphism in respect of plumage is determined predominantly by genetic factors. From them no evidence could be derived which would suggest that the difference in plumage colour on the two sides of the body was the result of any interplay between feather growth-rate and hormone threshold. It is not surprising, in the light of the results obtained from the implantation of œstrin and testosterone, that Zawadowsky's (1926) castration experiments on the finch failed to provide any convincing proof of any hormone control of plumage-type.

The third gynandromorph is a fowl (D) which came into our possession as long ago as 1932, when it was received as a gift from the Sterling Poultry Products Limited, near Andover, Hampshire. It was then a partly grown pullet, or at least it was regarded as a pullet, out of the mating Light Sessex hen × Rhode Island Red cock. It was remarkable at that time for the reason that whilst its left leg and left side of the body were white, its right leg and the right side of the body were yellow. The dividing line between white and yellow followed strictly the mid-line of the body excepting in the head, both upper and lower beak and both eye-rings being yellow. Although not very pronounced at the time, there was even then a definite lateral size asymmetry, the yellow side appearing larger and coarser. The head, derived embryologically from tissue of the same genetical constitution as the larger yellow side, was itself larger and coarser than that of the normal female of the same age. As the bird matured, this lateral size difference became more and more pronounced, until when fully grown the bird was markedly asymmetrical and possessed on the larger right side a large male-like spur. The average linear difference between the bones of the two sides was found later to be 13 per cent. Its gait was clumsy and limping, but the bird itself was quite healthy and proved to be a moderately good layer. In its second year it was mated to a Rhode Island Red cock and produced twenty-six chickens, all of which were golds. Ten were males and five were females, the sex of the remainder being unrecorded, as was also, unfortunately, their flesh colour.

When the bird was five she developed respiratory difficulties and was brought under close observation. Cloacal exploration revealed a large internal mass, situated dorsally and posteriorly to the ovary. It was thought that she had developed a tumourous growth which was pressing upon the peritoneal air sacs, and thus interfering with respiration. On April 6, when approximately five and a half years old, she was found attempting to lay a normal fully shelled egg. She was unable to extrude this, and it was broken and removed manually. During the next four months she remained in fairly good condition, though at times she suffered severely from dyspnœa. In September her condition became rapidly worse and she died, aged six.

The bird had been regarded throughout its life as a female showing considerable lateral size asymmetry. Her breeding record showed quite clearly that she was XY in sex-chromosome constitution, and that she had not received the dominant silver gene from her mother. When mature she did show an occasional whitish feather on the larger side of the body, but on closer examination these proved to be either very pale red or else white with flecks of red, and there was no greater difference between the coloration of the two sides of the body than can be found between full sisters out of the same mating.

It certainly was not expected that her internal genitalia would include male structures, and the desirability of any histological examination was not seriously considered. Her cadaver was kept in cold storage for several days. When it was dissected it was found that the bird had been laying internally and that a very large mass of egg material had accumulated, to become closely attached to the back and encapsuled by layers of fibrous tissue. This was the mass that had been identified as a tumour. There was an ovary in the normal resting condition, and on the right side there was a large testis-like organ. The left ovary measured 34 × 15 × 9 mm. and weighed 1·67 g., the largest follicles being 3 mm. in diameter. The right testis-like body had the appearance of the typical lobulated compensatory gonad described by Domm (1927) as growing after early ovariotomy, save that it was considerably larger, being 38 × 17 × 7 mm. and weighing 3·13 g.

Microscopical examination revealed few post-mortem changes. The ovary presented a normal structure and the testis-like organ consisted of spermatogenic tubules showing complete spermatogenesis, together with typical cavernous *rete* spaces, *ductuli efferentia* and epididymal tubules proper in its medial capsule, these being, according to Gray (1937), the typical components of the normal epididymis of the fowl. In view of this, and also of the fact that a compensatory right gonad is usually accompanied by a *ductus deferens*, it is reasonable to assume that a complete male accessory equipment existed in this bird.

The peculiar interest of this case lies in the fact that the sex-chromosome constitution of the male side of this avian gynandromorph could be recognised. It is of extreme importance to note that in tissue which possesses the typical female sex-chromosome constitution, male-type skeletal structures, including a large spur, testicular material that exhibits complete spermatogenesis and (presumably) male deferent ducts can occur.

The fourth case was that of a pure-bred Rhode Island Red fowl (E). Its owner, who regarded it as a curiosity, contributed the bird as material for a demonstration on post-mortem methods, which was being conducted by Mr T. E. Knowles, secretary of a Lancashire poultry breeders' association. The bird's neck had been dislocated before it was handed to Mr Knowles, who, as the autopsy proceeded, disclosed a testis on the larger right side and an ovary and oviduct on the left. In the uterus there was a fully formed egg, which was removed. The case was brought to our notice by Mr G. M. Robertson, Advisor in Poultry Keeping to the County of Lancashire, who had received the carcase and had preserved it in formalin. From Messrs Robertson and J. J. Green of the Lancashire Agricultural Education Department we received the preserved specimen on loan.

The bird exhibited typical Rhode Island Red feathering which was completely female save that there were a few male-type feathers on the sides of the saddle. Measurements of the long bones showed those of the left side to be 11 per cent. smaller than those of the right. Both legs were yellow, but the smaller one was distinctly paler in colour. There was a fully functioning ovary on the left with numerous full-sized yolks and a completely developed oviduct. On the right there was a small but typical testis measuring 19 × 9 × 6 mm. and a well-defined *ductus deferens*. Representative areas were removed from the testis and from the medulla of the ovary and examined microscopically. Though fixation was poor, the general structural features were plainly distinguished. No testicular tissue was found in the ovary. The right gonad was composed of spermatogenic tubules, in many of which normal spermatids and mature spermatozoa could be recognised.

There is general agreement concerning the cause of simple lateral asymmetry in birds. Hutt (1929 *a*) classified the recorded cases in the fowl into two groups: (1) those in which only pigmentary differences existed between the two sides, and (2) those in which lateral size asymmetry was also present. He suggested that the cause, in the case of group 1, was gene mutation; in group 2, chromosome elimination. Crew (1932), in describing a new case, in which one side was yellow and the other white, reviewed four cases previously reported, together with another mentioned by Knox (1931), in which both legs were white though one was marked with a yellow streak, and argued that it was possible to explain them all by an appeal to the chromosome elimination hypothesis alone. Crew and Lamy (1935) described sixteen colour "half-siders" in the budgerigar, and were able to show from the genetic evidence that the cause was in all cases the loss, in a heterozygote, of an autosome from that side of the body which exhibited the recessive character.

The test of the validity of this elimination hypothesis to explain lateral colour asymmetry and also lateral size asymmetry is most easily sought in an individual heterozygous for some plumage colour character. If there is the expression of a recessive character on one side of the body, then it should appear on the smaller side. The four new cases of simple lateral asymmetry presented in this paper can all be accommodated by the chromosome elimination hypothesis. If, in the canary, buff is accepted as the recessive allele of yellow, then, as the smaller side of the body is buff, it is reasonable to assume that the manifestation of this recessive character in a heterozygote and also the lateral size asymmetry are both due to the loss of the autosome carrying the dominant yellow allele of buff on the buff side of the body. In the case of the Old English Game bantam hen the lateral colour asymmetry can easily be explained by the loss from the right side of the autosome carrying the dominant allele of spangling at the first cleavage division. In the white-yellow-fleshed cockerels (B and C), since white and yellow epidermal pigmentation are based upon a single pair of autosomal alleles, white being dominant to yellow, the lateral colour and size asymmetry can be explained by postulating that the dominant white (W) gene had been lost from the soma on the yellow side of the body.

The case of Roberts and Quisenberry (1935) is not so easily explained. According to the argument employed thus far, the loss of an autosome from each side of the body might be expected to leave the size relationship of the two sides unaltered. The left side of this bird resembled the father, a light Brahma, whilst the right side had, in general, the characterisation of the mother, a Barred Plymouth Rock. The right side was the smaller, showed pigmented barred feathers and a clean shank. The left side was the larger, had white feathers, except in the neck, wings and tail, and the shank on this side was feathered. Presumably the bird was heterozygous for barring, peacomb, feathered shank and the pigment extension factor, being Bb, Pp, Ff, Ee. Since the few feathers on the left side that were pigmented were barred and the comb was pea on both sides, the factors Bb and Pp presumably pursued a normal distribution. The authors interpret the case as the result of the loss of two autosomes, one carrying the gene for feathered shank (F) from the right side, and the other carrying the gene (E) from the left. They explained the very large lateral size difference by suggesting that there are a greater number of size genes on the chromosome carrying the gene for the feathered shank than upon that carrying the gene for pigment extension. This assumption was reasonably valid in view of the fact that the chromosome carrying the gene for feathered shank was derived from the larger of the parents, and therefore might have been carrying more positive size genes.

Be this as it may, it is certain that our fowl D cannot be explained by simple chromosome elimination, for the recessive yellow was expressed on the larger male-like side. We were forced to seek some alternative explanation. A review of all the cases known to us led to a recognition of the fact that those in which lateral size asymmetry had been noted fell into two quite distinct quantitative classes with respect to the lateral size differential. We therefore entertained the notion that possibly two different kinds of abnormality in chromosome distribution might be concerned in their causation. The first class, as far as the fowl is concerned, includes all cases of simple lateral asymmetry in which lateral size differences have not been noticed, or else on careful examination

Class I includes the following cases:—

TABLE II.

Case No.	Author.	Description.	Gonads.	Sex.	Cause.
1	Lambert (1929).	No size difference noted. Left side white-fleshed; right yellow.	Right nil?; left ovary.	XY	Elimination of autosome carrying W on the right. Right side w; left Ww.
2	Knox (1931).	As No. 1.	Not stated; probably normal ♀.	XY?	Elimination of autosome carrying W on the right. Right w; left Ww.
3	Knox (1931).	No size difference noted. Right shank green; left yellow.	Right nil; left ovary.	XY	Elimination of autosome carrying a on the left. Right aa; left a.
4	Crew (1932).	No size difference noted. Right shank white; left yellow.	Right nil; left ovary.	XY	Elimination of autosome carrying W on the left. Right Ww; left w.
5	Present case A.	No size difference noted. Right side spangled; left non-spangled.	Right nil; left ovary.	XY	Elimination of autosome carrying P on the right. Right p; left Pp.
6	Present case B.	Left side yellow-fleshed and 3 per cent. smaller than right white-fleshed side.	Right testis; left testis.	XX	Elimination of autosome carrying W on the left. Right Ww; left w.
7	Present case C.	Same as 6, with 2 per cent. lateral size difference.	Right testis; left testis.	XX	Elimination of autosome carrying W on the left. Right Ww; left w.

a = unidentified autosome.
W = autosome carrying the gene for white flesh; w = the autosome carrying w, the recessive allele for yellow flesh.
P = autosome carrying gene for the non-spangled character; p = the autosome carrying the recessive allele for spangled.

have been found to be of the order of 2–4 per cent. We suggest that the cause of the abnormality in such cases is the elimination of an autosome from one of the two daughter cells that result from the first cleavage division. The side of the body which exhibits the recessive character is always the smaller if lateral size differences exist. The second class includes all the fowls that have been described as gynandromorphs, together with the cases of Crew (1928) and Roberts and Quisenberry (1935). In them the lateral size differences are of the order of 10–15 per cent. We suggest that the cause of the abnormality in these cases is non-disjunction, one of the two daughter cells resulting from the first cleavage division being haploid in respect of a particular autosome, the other triploid. In such circumstances it is reasonable to expect that the side possessing the extra chromosome would show the effects of the interaction of three alleles. Whilst the haploid side would be smaller than normal, the triploid side would be larger, so that the resulting size differential is much greater than in a case of simple elimination. Moreover, those qualitative characters, the phænotypic expression of which depends on gene balance (Bridges, 1932), would be affected.

It is seen that all the cases in Class II have one feature in common: there is a great and easily observable difference in the size of the two sides of the body. It will be noted that we have proposed a combination of elimination and non-disjunction as an explanation of Roberts and Quisenberry's case. In the light of the new evidence now presented this seems a more reasonable interpretation of the lateral size differential than double elimination. Circumstances did not permit Roberts and Quisenberry to make skeletal measurements or to examine the gonads of their bird, but it is clear from the published photographs that the two sides of the body differed markedly in size and that the bird was a typical cockerel in appearance. The possibility that it possessed ovarian tissue cannot be ruled out however.

The large differences in size between the two sides of the body have been responsible in great measure for the primary identification and ultimate classification of the fowl gynandromorphs. It was this considerable lateral size difference, associated with the presence of a testis on the larger right side and ovarian tissue on the smaller left, which persuaded Macklin and Hutt to the view that the cause of this condition was the elimination of an X-chromosome. But our case D shows conclusively that it is possible for a female, XY on both sides of the body, to exhibit not only a lateral size difference of 13 per cent., but also to possess a functional testis on the larger right side and a functional ovary on the left smaller side. Elimination of an X is certainly not the cause

Class II consists of the following cases:—

TABLE III.

Case No.	Author.	Description.	Gonads.	Sex.	Cause.
1	Macklin (1923).	Left side 14 per cent. smaller than right. Male feathers in hackle only.	Right testis; left ovotestis.	XY	Non-disjunction involving the autosome carrying a. Right side aaa; left a.
2	Crew (1928).	Right side 15 per cent. smaller than left. Left side white-fleshed; right yellow.	Right testis; left testis.	XX	Non-disjunction involving the autosome carrying W. Right side w; left WWw.
3	Roberts and Quisenberry (1935).	Right side with barred plumage and clean shank. Left side much larger with white feathers and feathered shanks.	Unknown. Probably testis on each side.	XX	Elimination of autosome carrying E on the left, together with non-disjunction involving autosome carrying F. Right side Eef; left eFFf.
4	Vecchi (1936).	Left side predominantly white plumaged with feathered neck and 13 per cent. smaller than right side, which was brown-black and with naked neck.	Right testis; left ovotestis.	XX?	Non-disjunction of autosome carrying N. Right side NNn; left n.
5	Hutt (1937).	Left side 13 per cent. smaller than right, which showed scattered male feathers and slightly wider barring.	Right testis; left ovotestis.	XY	Non-disjunction of autosome carrying a. Right side aaa; left a.
6	Present case D.	Left side 13 per cent. smaller than the right. Left side white-fleshed; right side yellow.	Right testis; left ovary.	XY	Non-disjunction involving the autosome carrying w. Right side Www; left W.
7	Present case E.	Left side 11 per cent. smaller than right. Left shank a lighter yellow colour.	Right testis; left ovary.	XY	Non-disjunction involving the autosome carrying a. Right side aaa; left a.

E = autosome carrying the gene for the extension of melanin; e = the autosome carrying the recessive allele (lack of pigment).

F = the autosome carrying the gene for feathered shank; f = the autosome carrying the recessive allele for clean shank.

N = the autosome carrying the gene for naked neck; n = the autosome carrying the recessive allele for feathered neck.

of lateral asymmetry in this case. Nor is simple elimination of an autosome, for it is the larger side that exhibits the recessive character. A double autosomal elimination might be suggested, as it was in the case of Roberts and Quisenberry, if it is assumed that the chromosome eliminated from the smaller side carried the larger number of size genes. But there was no genetic evidence that more than one chromosome had been involved. Moreover, if it is postulated that elimination had occurred on the larger side, then it must be supposed that loss of one and the same chromosome can sometimes result in a decrease in size (cases B and C and that of Crew, 1928), and at other times yield an increase (case D). The use of a size differential as a criterion for gynandromorphism by Macklin and by Hutt was, of course, not unreasonable, for the latter (1928) had shown that in the fowl the male is larger than the female by approximately 12–15 per cent. But a larger size in itself is no real criterion for maleness, for Crew's (1928) case had a 15 per cent. lateral size difference and yet was completely male.

To offer a satisfactory explanation of the dual nature of the gonads in these cases is a difficult matter, concerning which it is possible only to speculate. It is established that the normally atrophic right gonad of the XY female fowl may be induced to differentiate under appropriate stimuli, and that, when this happens, the gonad usually develops into a testis-like organ. Further, it is known that the earlier in the life-history the appropriate conditions are provided, the more complete is the differentiation (Domm, 1927, 1929). Formerly it was thought that this fundamental duality existed only in the female, but the work of Wolff and Ginglinger (1935), Dantchakoff (1936) and of Willier, Gallagher and Koch (1937) has shown that the male also possesses asymmetric gonad-forming potentialities, the embryonic left gonad possessing ovarian cortical elements which, under appropriate circumstances, develop into ovarian tissue. It is apparent, however, that the male is the more stable of the two, the ovarian elements becoming manifest only when the necessary stimuli are applied very early in embryonic development, whereas the right gonad of the female can be induced to develop into testis-like tissue even after hatching. May it not be that the loss or gain of autosomal material provides the necessary stimuli for the development of the rudimentary right gonad in an XY individual, and possibly also for the development of the cortical elements in the embryonic left gonad of the XX individual? We would suggest that the association of demonstrable aberrant autosomal distribution and male-female genitalia found in these cases is not accidental, but that the maldistribution of the chromosomes is the cause of the gynandromorphism.

In Tables II and III there are to be found seven cases in which the white-yellow flesh autosome is involved. The reason why this chromosome figures so prominently is that the Light Sussex × Rhode Island Red cross is a very popular one. Since there are two sexes and two classes (due to elimination and to non-disjunction respectively, we suggest), there are four combinations: Class 1, male; Class 1, female; Class 2, male; Class 2, female. Disregarding Knox's case, in which the sex of the bird was not stated, the six flesh-colour mosaics can be classified as follows:—

Class 1, male.	Present cases B and C.
Class 1, female.	Lambert's case, Crew's (1932) case.
Class 2, male.	Crew's (1928) case.
Class 2, female.	Present case D.

It will be noted that none of the four birds in Class 1 possessed both male and female sex equipment; the elimination of the flesh-colour autosome did not affect the sexual characterisation of the individual, whether male or female. Similarly, maldistribution of this autosome left the sexual equipment untouched in the case of the male of Class 2, although it produced marked lateral size asymmetry. But the same kind of maldistribution in the case of the XY or genetic female of Class 2 was associated with a male sex equipment on the right side, and was, we submit, the cause of the gynandromorphism. It would seem that an extra autosome is sufficient to swing the cellular balance in the male direction and provide the stimulus for the differentiation of the right gonad.

If tissue possessing this extra autosome exhibits male organisation, then tissue haploid for this same autosome would be expected to be unbalanced in the female direction. But such an imbalance in female tissue would not produce recognisable modifications in the sexual characterisation, for this is already female (the cases of Lambert and of Crew, 1932), whereas in the male it might reasonably be expected to do so, particularly when it occurs in tissue ancestral to the left gonad which is known to possess ovarian potentialities. That this is not borne out by the facts (cases B and C) is not surprising when it is remembered that the stability of male tissue in the fowl is much greater than that of female tissue.

It is not unreasonable to assume that in the fowl the autosomes differ among themselves in respect of their sex-determining potencies, and that certain of them are so loaded with male-determining properties that they can switch the sex from female to male when one is gained, and from male to female when one is lost. Vecchi's case may indeed be an instance of this. The bird showed a lateral size difference of 13 per cent., but had a large male spur on each side. The comb was large, fairly erect and male-like. The internal genitalia consisted of a normal testis and a *vas deferens* on the right and an ovotestis on the left. There was no oviduct. The bird was thought to be a cross between a Leghorn and a Naked-neck, and was mottled white and brown-black on the left, brown-black with very little white on the right. The larger side had the dominant naked-neck character, the left side possessed normal hackle feathers which were male-like. The rest of the plumage was henny. In general appearance the bird was male-like. This masculine appearance, the absence of the oviduct and the fact that the left gonad was composed mainly of testicular tissue, suggest to us that this bird was XX in constitution, and that the loss of the naked-neck autosome from the left side had induced survival and differentiation of the ovarian elements of the embryonic left testis. Œstrin derived from the ovarian portion of the ovotestis was responsible for the henny-feathering. The lateral size differential places this bird in Class 2, for which non-disjunction is suggested as the cause. The N autosome was lost on the left and gained on the right. The lighter colour of the left side can readily be explained by the loss of pigment-producing or pigment-intensifying genes linked with N.

Simple elimination in this case would have produced the left ovotestis and the female feathering but very slight lateral asymmetry, according to the hypothesis which we are now presenting, with the result that this bird would have closely resembled the so-called hermaphroditic fowl, *e.g.* those described by Boring and Pearl (1918) and by Hartmann and Hamilton (1922). It may be that such abnormality is the result of simple elimination of an autosome in an XX individual, and that intersexuality in the fowl is commonly caused by maldistribution of the chromatin material. On the other hand, Vecchi's case may be an instance of the conversion of an originally XY individual into a gynandromorph by non-disjunction, though this explanation does not account for the spurs or for the absence of the oviduct. It is impossible to state what the sex-chromosome constitution of the bird was, but the naked-neck autosome is certainly concerned in the production of the abnormality in this bird, and provides sufficient evidence to permit us to submit that since non-disjunction of an autosome is the cause of the gynandromorphism in case D, a similar aberrant chromosome distribution is also responsible for the same condition in Vecchi's fowl.

All the observations concerning white and yellow epidermal pigmentation can be conveniently explained if it be assumed that $W > w$ but that $W < ww$. In case D, for example, the left side is genetically W and white, whilst the right is Www and yellow. Crew's 1928 case was WWw on the large side and therefore white, whereas the smaller side was w. The cases of Macklin and Hutt, and also the present case E, were pure breds, and therefore not pigment mosaics. But, since they all showed size and sex-equipment asymmetry similar to that in case D, it is likely that they may all be due to non-disjunction of this same white-yellow autosome. The difference in the shade of yellow on the two legs of case E strongly supports this suggestion. The larger shank was a deeper colour, as would be expected if the larger side were www and the smaller w.

It is true that the left gonad in Macklin's and Hutt's cases included testicular tissue, but this could have been derived from the triploid cells of the right, which had become incorporated in the cortical elements of the left ovary, for it is established that the primordial cells of the differentiating gonad wander considerably and may be derived from either side. Confirmation of this is found in the results of the breeding tests in which fowl C was used, for these showed that the constitution of the testis did not necessarily correspond to that of the soma of the same side.

The lateral difference in respect of width of barring in Hutt's case is probably due to the action of modifying ground-colour genes carried on the misbehaving autosome, or else to a differential in feather growth-rate such that a greater feather length is formed during a physiological cycle of one bar. The occasional male feathers on the large side are probably to be explained on the basis of Lillie's (1931) hypothesis.

When the gain is on the left side, *e.g.* the pheasant first reported by Bond (1913) and re-examined by Huxley and Bond (1934), in which there was a great deal of overlapping and intermingling of plumage types, much of it being intersexual, the medulla of the left gonad does not, as is normally the case, degenerate completely, but develops into a medullary testis to yield an ovotestis. If, in such a case, there is a gonad on the right smaller side, it would presumably be testicular and be derived from the primordial triploid cells of the left. In all cases in which both fully differentiated testicular and ovarian tissues are present, the time is reached in development when the male and female sex-hormones take charge of the further sexual differentiation of the Wolffian and Müllerian duct derivatives, and the final result can be a complete male equipment on one side and a complete female equipment on the other. But the work of Greenwood and Blyth (1930) indicates that, if the testis were fully active in such a bird, the ovary would be limited in its functioning.

The pedigree of case D enables us to eliminate many of the possible alternative explanations of gynandromorphism. An egg with two nuclei, each of which became fertilised by a separate sperm, could not account for this case, for both sides were not white-fleshed. It does not seem reasonable to assume that one of the nuclei of such an egg remained unfertilised to give rise to one side of the body, this being haploid, for both sides are gold, and therefore each must possess the paternal X-chromosome. One side can hardly be haploid and paternal in derivation as a result of polyspermy, since then the haploid side would be the smaller side, whereas the smaller side is the left, which exhibits the maternal white-flesh character. The large side might conceivably be haploid and paternal, but, if this is so, then the case of Crew (1928), which involves the same type and degree of size and flesh-colour asymmetry, and which was also the result of a Light Sussex × Rhode Island Red mating, must be due to some other cause, because the large haploid side is here white-fleshed, and thus maternal. So that we must assume either that in the one case the haploid side is the larger and in the other it is the smaller, or else that it is paternal haploid tissue in one case and maternal in the other. But while Crew's case showed the dominant silver of the mother on both sides, many gold feathers, a paternal character, also occurred on both sides. This partially suppressed display of recessive gold is characteristic of the normal male out of this cross, and Crew's bird therefore possessed both maternal and paternal chromatin on both sides, and could not have been haploid.

We have shown that the lateral differences in plumage coloration in the Gouldian finch are determined by genetic, rather than by hormonal, factors. This being so, it is necessary only to assume that when the cellular constitution is altered in the male direction by somatic heteroploidy the plumage is also altered. If this is so, then the finch gynandromorphs are due to non-disjunction rather than to elimination. The brilliant-coloured side of the finch gynandromorph is the larger side, and *a priori* this must be the trisomic side in the case of non-disjunction or the normal side in the case of elimination. Elimination is hardly possible, for then the bird would have to be a male originally, and the loss of an autosome must yield female feathering on the smaller side, whilst the internal genitalia should be predominantly or wholly male. But these birds were females, judged by their internal genitalia. The fact that these finches do not exhibit a 15 per cent. lateral size difference, as in the fowl, is no argument against the non-disjunction hypothesis, since in the finch, with its own peculiar chromosomal constitution, elimination and non-disjunction need not produce the same quantitative effects as they do in the fowl. There is no considerable size difference between male and female in the finch, and so the addition of an autosome to one side would not be expected to alter the size relationship of the two sides materially. The actual size difference found in these finches was of the order of 3–4 per cent. If non-disjunction is the cause, then elimination would be expected to yield either no difference or else an undetectable one. The slight increase in size of the side with the extra autosome following non-disjunction would seem to be due to the action of additional size genes.

SUMMARY.

1. Four new cases of lateral colour asymmetry in birds are recorded: a yellow-buff cock canary, a spangled-partridge Old English Game bantam hen and two yellow-white fleshed F_1 cocks *ex* Light Sussex hen × Rhode Island Red cock.

Four new cases of gynandromorphism in birds are described: two in the Gouldian finch; two in the fowl.

2. It was found that all the mosaic birds examined showed lateral differences in respect of size, those in the fowl falling into two classes: (1) that in which the difference between the two sides was of the order of 2–4 per cent.; (2) that in which this difference was 10–15 per cent. While in many cases measurements are not given, it seems likely that all cases reported in the literature belong to one or other of these classes.

3. It is suggested that in the fowl the birds in Class 1 are instances of the elimination of an autosome, and that in those of Class 2 non-disjunction resulting in bilateral heteroploidy has occurred, there being a gain of an autosome on the larger side, its loss on the smaller.

4. It is suggested that heteroploidy provides a complete explanation of gynandromorphism in the fowl.

5. It is argued that the gynandromorphic finch, a genetic female with male coloration on the slightly larger right side (3–4 per cent.) and female on the smaller left, and with an ovary on the left and no testicular tissue anywhere, is to be explained by non-disjunction rather than by simple elimination. It is shown that, in the Gouldian finch, male and female coloration are purely genetic characters, and that hormones play little or no part in their origin and maintenance.

6. Spangling in the Old English Game bantam is shown to be a monogenic autosomal recessive.

7. It is concluded that lateral gynandromorphism in birds is always the result of an aberrant chromosome distribution, that it is always associated with lateral size differences and that there are three types:

(1) The sparrow- or finch-type, in which the plumage characterisation is genetically determined and follows the aberrant lateral chromosome distribution.

(2) The fowl-type, in which the sex-dimorphic plumage characterisation is subject to hormonal regulation, and so bilaterality of plumage type is practically an impossibility.

(3) The pheasant-type, in which a nearly normal sex type of plumage occurs on one side and an intersexual type on the other.

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DESCRIPTION OF PLATE.

Gouldian finch possessing male plumage on the right side and female on the left.

(*Issued separately June* 8, 1938.)

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Neill & Co., Ltd.

X.—The Anatomy of the Polychæte *Ophelia cluthensis* McGuire 1935. By Robert S. Brown, B.Sc., from the Department of Zoology, University of Glasgow. *Communicated by* Professor Edward Hindle, Sc.D. (With One Plate and Thirty-three Text-figures.)

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INTRODUCTION.

Ophelia cluthensis is a Polychæte worm which has been known for some years from specimens taken from the sands around Millport, and particularly from Kames Bay. It was described for the first time by McGuire in 1935, and its general appearance may be seen in the Plate, figs. A, B.

Fauvel (1925) describes a small *Ophelia* which he found in the sand at Saint-Vaast in 1899, and which he identified as a young *O. limacina.* His brief description, however, corresponds with that of the worm here described in the number of setigerous segments, and the number and position of the gills, as well as in its size, and it is probable that it was actually *O. cluthensis.*

The family Opheliidæ is a small one, upon which, apart from the early morphological work carried out by Claparède, de Saint-Joseph and Kükenthal, little seems to have been done. It is hoped, therefore, that this paper will be of some assistance in adding to our knowledge of this interesting group.

HABITS AND DISTRIBUTION.

O. cluthensis occurs most abundantly in the sand just below High Water Neap tides, where it is found burrowing beneath the surface, probably just deeply enough to escape the shifting of the surface sand due to wave action. In Kames Bay it is most plentiful at a depth of about two inches, and little difference is noticed in its position during rainy weather.

It may often be seen when a little pool is made in the sand by digging a hole and allowing this to fill with sea-water. As the hole fills, specimens may be washed out of the sand as this crumbles away at the edge of the pool. The worm burrows beneath the surface immediately it settles on the bottom. Very often the worms, when washed out of the sand, are surrounded by sand grains which adhere closely to the body, held there by mucus which is exuded by the worm. This is especially noticeable with the smaller specimens, so that they are not easily seen. Specimens removed from the sand assume a flat spiral form, and it is a matter of some difficulty to make them straighten out for purposes of examination and section-cutting.

A quantitative investigation of the distribution of the worms down the beach in a seawards direction was made as follows:—

The sand inside a 15-in. square was removed to a depth of about 3 in., and passed through a sieve of 1-mm. gauge. The finer sand grains passed through, and the worms were retained along with the coarser grains. The contents of the sieve were immediately washed into jars, and the worms sorted out and counted. This was done for stations at regular intervals down the beach.

It was thought that some of the worms, which are often less than 1 mm. in diameter, might pass through the sieve, but it was found that this was so only if they were allowed to settle, and an examination of sifted sand produced no further specimens.

The figures given below are probably, therefore, a good approximation to the actual numbers of the worm present in the sand at the place investigated. The counts were made on April 7, 1937. Ten stations were taken at 5-yard intervals down the beach, the worms not being found beyond these limits. Since the worms were all either ripe or nearly so, it was possible to distinguish the sex.

The figures obtained were:—

Station No.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
No. of ♂♂ . .	0	1	9	62	37	35	13	10	7	0
No. of ♀♀ . . .	0	0	9	52	35	32	10	11	6	0
Total . . .	0	1	18	114	72	67	23	21	13	0

Intertidal range 180 yd.

Fig. 1 illustrates this zonation graphically.

From the above table, it will be seen that the sexes are almost equally represented, the males only slightly outnumbering the females. Also, the figures give some idea of their abundance. At their maximum density, 114 worms were taken from the 15-in. square sample, while at no station were there more than a dozen Polychætes of other species. This suggests that *Ophelia cluthensis* plays an important part in the ecology of the beach.

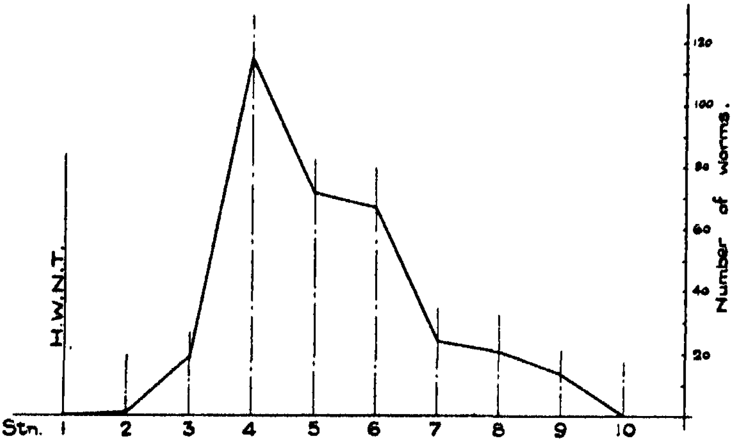


FIG. 1.—Zonation of *Ophelia cluthensis* in Kames Bay.

The specimens taken from Stations 4, 5, and 6 were found to be more advanced in their development than those taken from elsewhere.

A similar survey was made by Dr A. C. Stephen of the Royal Scottish Museum, in Kames Bay, on September 24, 1935. His stations were 40 yd. apart, Station 1 being at High Water Neap tide mark. His results were:—

Station No.	1.	2.	3.
No. of worms per sq. metre	10	273	0

Dr Stephen also made counts on Fairlie sands on June 3, 1937, at stations 100 yd. apart, and his results were:—

Station No.	1.	2.	3.	4.	5.
No. of worms per sq. metre	6	26	28	22	0

Intertidal range about 1500 yd.

A survey of the beach at Kames Bay was undertaken by Mr Richard Elmhirst, of Millport Marine Biological Station, on June 7, 1937, in order to investigate the area occupied by the worms along the beach. On this date they were only found in any numbers within a belt 20 to 25 yd. wide, almost from one end of the beach to the other (fig. 2).

It is difficult to account for this restricted distribution. Wohlenberg (1937), in his researches at Königshafen, Sylt, has found *O. cluthensis* there to be similarly restricted. He finds it most abundantly on a sand-bank, which it occupies along with *Scolecolepis squamata* to the almost complete exclusion of other species. This sand-bank is composed of a clean coarse-grained sand which is very unstable, and Wohlenberg suggests that this instability of the sand is the main reason for the absence of other species and for the large numbers of *O. cluthensis*.

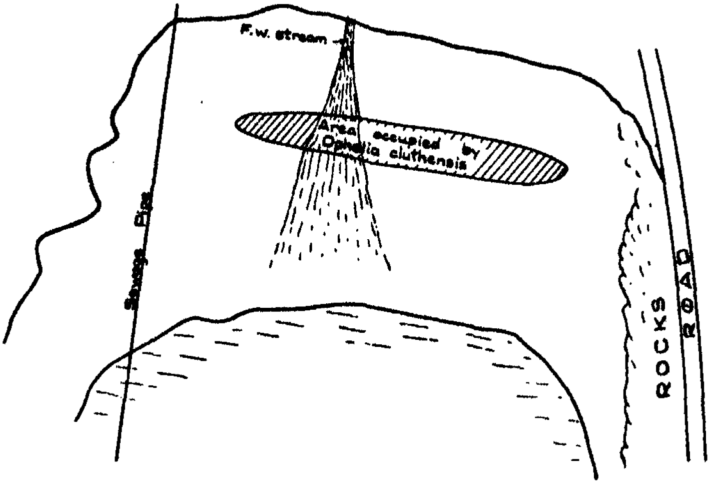


FIG. 2.—Sketch of Kames Bay showing distribution of *Ophelia cluthensis.*

At Millport and Fairlie, however, the sand is fine-grained and quite firm, so that here at least there must be some other limiting factor.

Besides the localities mentioned, *O. cluthensis* has been found at Aberlady, Firth of Forth; Balloch Bay, Cumbrae; and White Bay, Cumbrae. The species is, however, probably much better represented on British coasts than this small list would indicate, and should be found occupying the upper third of the Neap tide range in beaches having a clean surface sand. It has probably escaped notice so far because of its small size and narrow zonation.

It is interesting to note that in Kames Bay the belt crossed the small stream which spreads over the beach towards the west end of the bay, and indeed the larger specimens seemed to be most plentiful in the track of the stream. This, however, may possibly have been due to the fact that those beneath the fresh water were more expanded than those elsewhere.

Examination of the contents of the alimentary canal of the worms indicates that they feed on organic matter which they find in the sand, and which is taken in with the sand grains which the animals are constantly swallowing.

Nearly every specimen I have examined has been infected with a large number of gregarine parasites, which can be seen in sections attached to the epithelium lining the anterior end of the intestine.

METHODS AND TECHNIQUE.

The worms were kept alive in shallow glass dishes which were filled to a depth of about 2 in. with sifted (but unwashed) sand. It was found that the use of sifted sand was necessary, as worms kept in the mixture of coarse sand and beach shell debris in which they were collected soon died, due to the difficulty they experienced in burrowing. Rapid decomposition of organic matter in this mixture was also partly responsible. The glass dishes were placed in a large tank filled with sea-water to a depth of about 6 in., and this was kept well aerated. No arrangement was made in the tank to give a tidal effect, as the worms were found to live quite well without it. Indeed, many of the worms survived for about eight months under these conditions. One essential was coolness, and a prolonged spell of warm conditions in the tank was generally accompanied by a high mortality.

Removal of Sand Grains from Alimentary Canal.—In an endeavour to remove the sand grains from the alimentary canal before sectioning, the worms were kept for a few days in clean sea-water before fixing; but although many sand grains were voided during this time, few worms had a completely sand-free gut. It was thought inadvisable to leave them for a longer period, as they occasionally showed signs of internal disintegration after prolonged periods without food, and they could not be induced to feed on soft matter alone. Portions of the alimentary canal in some specimens were found to be free of sand after a period in clean sea-water, and these portions were employed for sectioning.

Narcotising.—Various narcotising reagents, *e.g.* chloral hydrate, menthol and absolute alcohol, were tried, but none was entirely satisfactory.

For examination of the external features of the worm, fresh water was the most useful, as this was the surest method of causing them to expand. It is evident that the expansion of the body is in this case due to turgidity as a result of osmosis, and for this reason specimens so expanded were not used for sectioning. The worms can, however, survive immersion in fresh water for a considerable period without undue harm, for they recover their normal powers of movement on reimmersion in sea-water. This faculty must obviously be correlated with their mode of life in the sand, where the salinity of the water at a depth of about 2 in. must be reduced after a period of wet weather at low tide. Indeed, the worms, as has been shown, occur in Kames Bay under a fresh-water stream, where the salt content must be considerably lower than that of sea-water. Reid (1930) has given the salinity for different depths in sand under a similar fresh-water stream in the intertidal zone, and while his figures show that this is almost equal to that of sea-water at a depth of about 10 in., at 2–4 in. it shows a considerable decrease.

Sectioning.—The best results for microscopic study were obtained by fixation in Bouin's fluid and clearing in cedarwood oil. Sections were cut at 10 μ.

Staining.—The most satisfactory stain for general purposes was Ehrlich's hæmatoxylin, counterstained with eosin, and most of the sections were stained in this way. Mallory's triple stain was also used. Intra-vitam staining with Grübler's methylene blue was tried, but with poor results. This stain is useful, however, for showing the number of setigerous segments of live specimens, as the chætæ take up the stain very quickly, and those of the first segment, normally difficult to distinguish, become at once apparent.

Whole mounts were stained with borax carmine.

Dissections.—These were carried out on freshly killed material, and on preserved specimens under 70 per cent. alcohol, in a solid watch-glass half-filled with blackened paraffin-wax. The finest obtainable entomological pins were used to pin out the body-wall. The small size of the worms and their tough body-wall necessitated the use of a binocular microscope and great care in dissection. The best results were obtained from individuals that were either immature or had shed their ova or sperms.

Dissections were stained with borax carmine and mounted for further examination.

EXTERNAL FEATURES.

Ophelia cluthensis varies in size within fairly wide limits. The adult males when expanded commonly range from about 9·5 mm. to 15 mm. in length, and the adult females from 11 mm. to 18 mm., but exceptionally large specimens up to 20·5 mm. have been found. The breadth ranges from about 0·9 mm. to 1·3 mm.

When taken from the sand the worms have a pinkish colour, due to the hæmoglobin of the blood showing through the translucent body-wall. The males are almost indistinguishable from the females to the naked eye, although the larger females, if they are ripe, are unmistakable, for they show numerous white patches. These patches are masses of eggs which lie free in the body cavity, and which are continually in motion, surging backwards and forwards with the movements of the animal. The ripe males present a more diffuse general whiteness, due to the concentration of sperms in the cœlome.

When examined by reflected light, the skin is seen to be iridescent. The cuticle exhibits very fine striæ running in a regular manner diagonally across the surface in both directions, and crossing at right angles (fig. 10), and it seems probable that these are responsible for the iridescence. There are no pores in the skin such as those described by de Saint-Joseph (1898) in *O. neglecta.*

The cuticle, 4–6 μ in thickness, covers the body-wall, and it is quite translucent, the larger blood-vessels being distinguishable through it. The great blood sinuses which surround the alimentary canal, particularly the intestinal blood sinus, give the worm its pinkish colour. Often the stomach shows as a dark patch lightly tinged with red (Pl., figs. A, B, *St.*). This dark colour does not appear to be due to the stomach contents, for specimens with apparently empty stomachs exhibit it; nor does it appear to be due to the structure of the stomach wall, as sections of this show no trace of pigment.

Some specimens have a bluish or purplish tinge. This may be due to a deterioration in their condition, as many specimens change to this colour after a period in captivity under unfavourable conditions.

The body is composed of 25 segments, the first 24 of which bear setæ (Pl., figs. A, B). It is divided into two parts of unequal length—an anterior more or less cylindrical part, swollen, tapering anteriorly, and terminating in the pointed head. This region comprises eight setigerous segments, and extends backwards to about one-third of the length of the animal from the head. The division between the two parts of the body is not abrupt, however, and may be farther back. This is due to the fact that the oblique muscles in this region may be relaxed, thus temporarily giving the ninth, and perhaps even the tenth, segment a cylindrical form.

The second part is narrower, and comprises the posterior two-thirds of the body. It is composed of 17 segments, and includes all those bearing gills. It is rounded dorsally as in the first region, but there is a deep furrow on the ventral side (Pl., fig. B, *V.gr.*). This posterior furrow, characteristic of the genus, is caused by the attachments of the oblique muscles (fig. 9, *Ob.m.*) along each side of the mid-ventral line. These muscles when contracted are responsible for the appearance of two large folds, which extend along the whole posterior end of the animal, one on each side of the ventral groove (Pl., fig. B, *L.v.f.*).

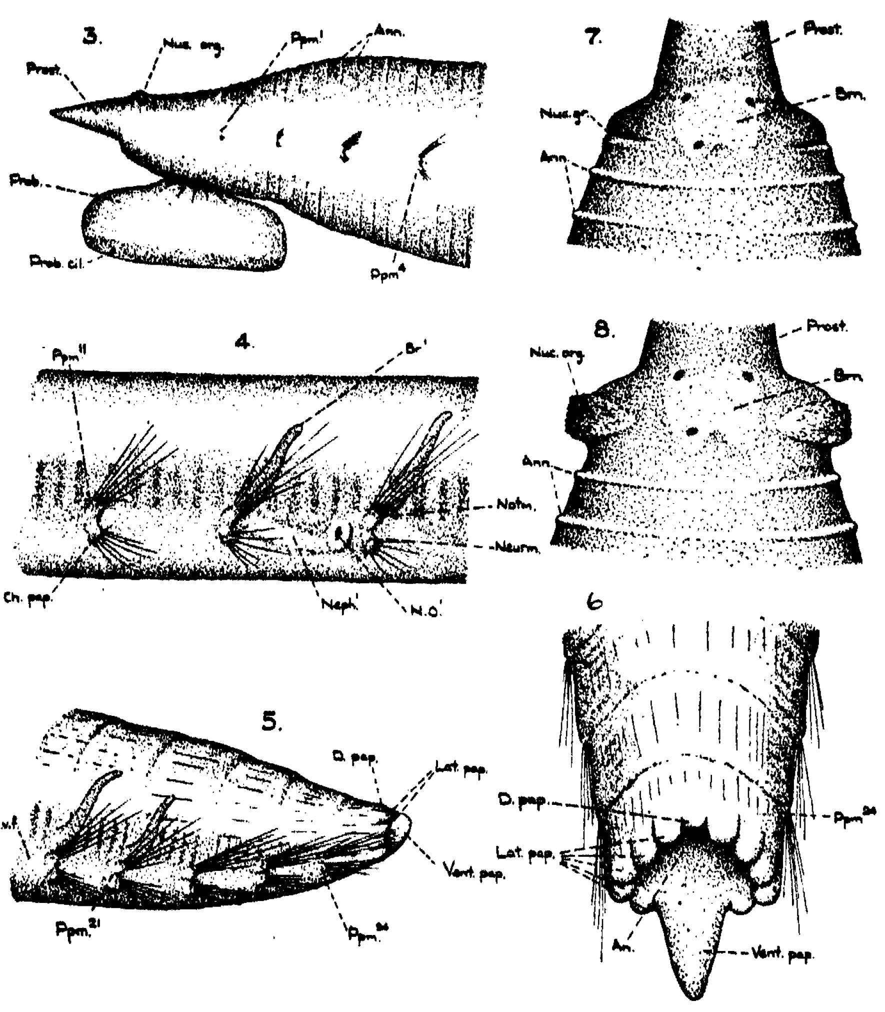
There are usually nine pairs of gills (Pl., fig. A, *Br.*^{1}–*Br.*^{9}) borne on segments 12 to 20, but specimens with eight pairs of gills, borne on segments 13 to 20, are not uncommon, while a few have 10 pairs, on segments 12 to 21. In specimens with 10 pairs, the first pair is generally small. Posterior to the gill-bearing segments is a short, highly retractile region of 5 segments; the first four are setigerous, while the anal segment is achætous.

The prostomium (Pl., fig. A, *Prost.*) is small, about 0·6 mm. in length, and is conical in shape. It is fairly mobile, being well supplied with muscles, and this, together with its stiffness, renders it a very useful burrowing organ. At the base of the cone the bilobed brain can be seen through the body wall (Pl., fig. A, *Brn.*). Embedded in the substance of the brain there are three eyes, readily visible with a lens as black spots. These eyes represent the two anterior and the left posterior eyes, the right posterior eye being absent in this species.

The conical head expands posteriorly, more or less abruptly, to join the first setigerous segment. At the anterior end of this segment there is a groove on each side running dorso-ventrally (fig. 7, *Nuc. gr.*). This is the nuchal groove, formed by the invagination of the nuchal organ, which will be described later. The first segment enlarges in diameter from the head backwards, and extends to the mouth (Pl., fig. B, *Mth.*), which is placed at the posterior extremity of this segment. The mouth-opening is a transverse slit of about 0·35 mm. in width, and possesses an anterior and a posterior lip. Anterior to the mouth is a smooth elongated triangular region, slightly more convex transversely than the general body surface, and bounded by a pair of shallow grooves which run round the sides of the mouth and forward to the head. These grooves also enclose behind the mouth a smaller triangular area, at the posterior end of which they unite and the shallow groove thus formed runs backwards along the mid-ventral line into the posterior ventral furrow. The segment is encircled by about ten little annuli, although this number is variable. These annuli are bounded by thickenings of the cuticle, rounded in section (fig. 13, *Ann.*), and these are very definite in this region of the body. Two small pits sometimes show in the dorsal body wall on each side of the middle line at about the seventh annulus. These are formed by the attachments of the labial muscles.

At the hinder limit of the first segment on each side are two groups of chætæ, a dorsal and a ventral in each case, but closely approximated (fig. 3, *Ppm.*^{1}). The chætæ of this segment are very small, and often difficult to distinguish, and a few specimens have been found in which they were entirely absent on one side.

The remaining segments of the anterior region are all more or less



FIGS. 3–8.—*An.*, anus; *Ann.*, annular thickening of cuticle; *Br.*^{1}, first gill; *Brn.*, brain; *Ch. pap.*, chætal papilla; *D. pap.*, dorsal anal papilla; *Lat. pap.*, lateral anal papilla; *L.v.f.*, latero-ventral fold; *Neph.*^{1}, first nephridium; *Neurm.*, neuropodium; *N.O.*^{1}, external opening of first nephridium; *Notm.*, notopodium; *Nuc. gr.*, nuchal groove; *Nuc. org.*, nuchal organ; *Prob.*, proboscis; *Prob. cil.*, ciliated portion of proboscis; *Ppm.*^{1}, *Ppm.*^{4}, etc., first and fourth parapodia, etc.; *Prost.*, prostomium; *Vent. pap.*, ventral anal papilla.

FIG. 3.—Side view of head end showing proboscis fully extruded. (× 23.)

FIG. 4.—Side view of middle of worm including segments 13 and 14. (× 23.)

FIG. 5.—Side view of hind end of a specimen with ten pairs of gills. The anus is in its normal closed position. (× 23.)

FIG. 6.—Anal region widely open, viewed from above and behind. (× 41.)

FIG. 7.—Dorsal view of head showing the nuchal grooves formed by the retracted nuchal organs. (× 59.)

FIG. 8.—Dorsal view of head with nuchal organ extruded. (× 59.)

similar to each other, having five or six little annuli, and bearing at the hind end of each segment two groups of chætæ, similar to those of the first segment, but becoming progressively larger in the succeeding parapodia.

Towards the posterior end of this region the annuli become less conspicuous, owing to the fact that the cuticular thickenings become less distinct and finally disappear, so that internal structures give the only indication of the subdivision of segments.

The ninth, tenth and eleventh segments are similar to the eighth except for the appearance of the latero-ventral folds, which bear the chætæ. The gill-bearing segments follow, and in these the gills and chætæ are borne on the latero-ventral folds (fig. 4). The gills are simple tubular structures, filled with blood and consequently red, usually held pointing upwards and backwards, and the chætæ emerge from the body wall just ventral to the gills.

In segments 13, 14 and 15, on each side just anterior to the chætæ, there is a small pore (fig. 4, *N.O.*^{1}), which is situated on a small papilla. These are the external openings of the three pairs of nephridia, which may be seen through the body-wall as whitish areas.

The chætæ of the middle region (fig. 12) are simple structures, about 0·8 mm. long in the notopodium and 0·6 mm. long in the neuropodium. They are about 8 μ wide and taper gradually to a fine point. They are brittle, and when seen under a high magnification are found to be striated along their length. They are thus similar in structure to those of *O. limacina* figured by McIntosh (1915). Where each group of chætæ leaves the body wall there is a small papilla (fig. 4, *Ch. pap.*), and this is most marked in the segments of the posterior region. Smaller curved bristles occur at the base of the chætæ, and these may be growing chætæ which are destined to replace the larger ones.

The four posterior setigerous segments show a successive tapering towards the anus, and are very retractile. Their chætæ are often slightly longer than those of the middle region, although similar in structure.

The anal segment is achætous, but bears at its posterior extremity twelve papillæ surrounding the anus (fig. 6). There is a small dorsal papilla (*D. pap.*), a single large ventral papilla (*Vent. pap.*), and five lateral papillæ (*Lat. pap.*) on each side. McGuire (1935) describes *O. cluthensis* as having nine small and two large anal papillæ, but in all the material I have examined there has been only one large anal papilla, although occasionally variations in the number of lateral papillæ have occurred. The ventral papilla is a direct continuation of the latero-ventral folds, which fuse in the pre-anal segment.

Ophelia cluthensis thus differs from the other species of *Ophelia* described by Fauvel (1927), as these all have two large ventral papillæ, quite separate and distinct. Another specific feature is the fact that the lateral and dorsal papillæ of this species are much shorter than those of other species, in which the anal papillæ are all more or less elongated.

The circular muscles of the anal region are contracted in the normal state, and the papillæ are thus drawn together around the anus. The ventral papilla bends dorsally and closes the anus like a valve (fig. 5). There is no trace of a membrane enclosing the anus, such as that described by de Saint-Joseph (1898) in *O. neglecta.*

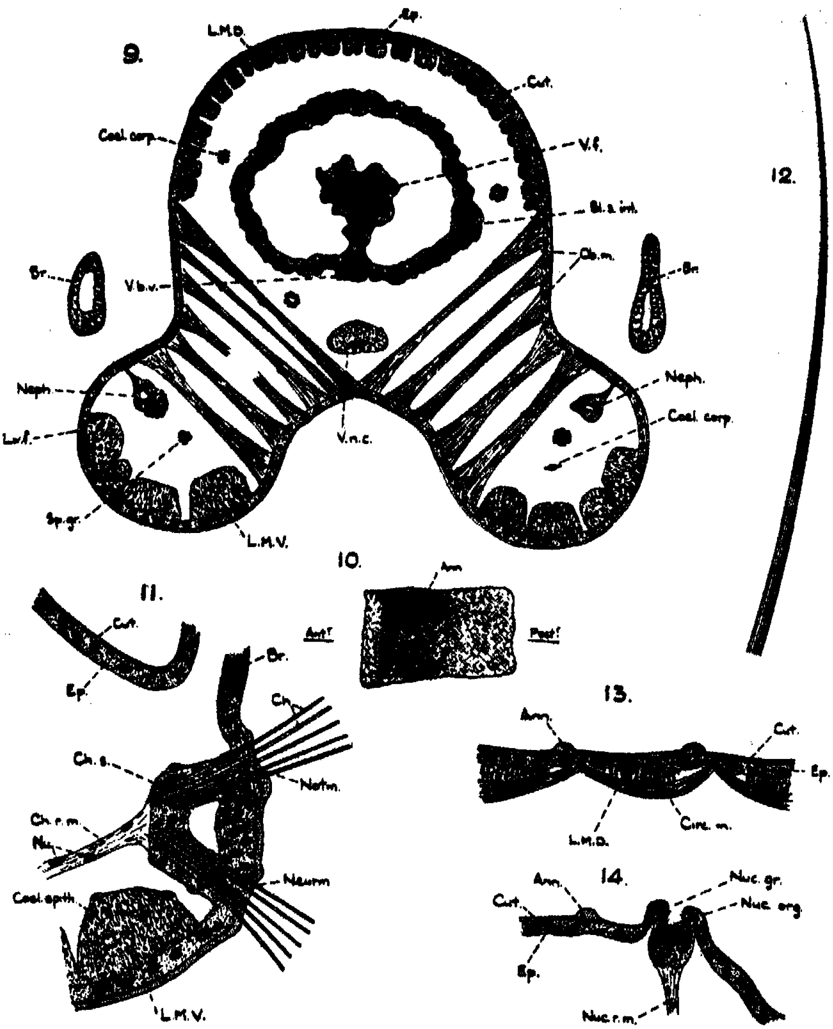
INTERNAL ANATOMY.

Musculature.—Underlying the epidermis, circular muscles occur only in the anterior region of the body, and in the last few segments. Anteriorly, they run in bands around the body between the annuli (fig. 13, *Circ.m.*). The dorsal longitudinal muscle bands run along the whole length of the body, and lie internal to the circular muscle bands, between which they are connected to the epidermis (fig. 13, *L.M.D.*). Along each side of the body there is an area in which the longitudinal muscles are not apparent, and in this region the chætæ are inserted (fig. 9). The ventral longitudinal muscles are best developed in the posterior region of the body, where they form the thick trunks traversing the ventral side of the lateral folds (fig. 9, *L.M.V.*). They run forward uninterruptedly, however, into the anterior part of the body, where they split up into smaller bands more comparable in size with the dorsal muscles.

The large oblique muscles occur in the middle and posterior regions of the body. As has been noted, they are responsible for the characteristic shape of the worms, for when they are relaxed the worms become cylindrical throughout their length. They run from the ventral side of the body to the sides, five or six bands in depth, commencing at the mid-ventral line (fig. 9, *Ob.m.*). These, together with the ventral muscles, are obviously the most useful in burrowing.

Each chæta-sac has attached to its inner surface a pair of short protractor muscles which run to the body wall anteriorly and posteriorly to the sac. They also have a retractor muscle (fig. 11, *Ch.r.m.*), which is attached to the body wall close to the mid-ventral line.

There are two pairs of retractor muscles for the eversible proboscis, and they are attached to the dorsal body wall. Retractor muscles for the nuchal organ are also present (fig. 14, *Nuc.r.m.*), and these are attached to the ventral side of the first segment on the side of the body opposite



FIGS. 9–14.—*Ann.*, annular thickening of cuticle; *Bl. s. int.*, intestinal blood sinus; *Br.*, gill; *Ch.*, chæta; *Ch. r. m.*, chætæ retractor muscle; *Ch. s.*, chæta-sac; *Circ. m.*, circular muscle; *Coel. corp.*, cœlomic corpuscle; *Coel. epith.*, cœlomic epithelium; *Cut.*, cuticle; *Ep.*, epidermis; *L.M.D.*, dorsal longitudinal muscle; *L.M.V.*, ventral longitudinal muscle; *L.v.f.*, latero-ventral fold of body; *Neph.*, nephridium; *Neurm.*, neuropodium; *Notm.*, notopodium; *Nu.*, nucleus; *Nuc. gr.*, nuchal groove; *Nuc. org.*, nuchal organ; *Nuc. r. m.*, nuchal retractor muscle; *Ob. m.*, oblique muscle; *Sp. gr.*, group of developing spermatozoa; *V.b.v.*, ventral blood-vessel; *V.f.*, ventral fold of intestine; *V.n.c.*, ventral nerve cord.

FIG. 9.—Transverse section through the fifteenth segment of the body of a male (semi-diagrammatic). (×64.)

FIG. 10.—Small portion of cuticle from the anterior region of the body. (×620.)

FIG. 11.—Thick transverse section through the parapodium of one of the gill-bearing segments (semi-diagrammatic). (×125.)

FIG. 12.—Distal half of a notopodial chæta. (×310.)

FIG. 13.—Longitudinal section through the dorsal body-wall at the anterior end of the worm. (×145.)

FIG. 14.—Longitudinal section through the nuchal organ, half-extruded (section slightly diagonal). (×110.)

to the organ it controls. The two muscles cross one another at their middle. The head is provided with a complicated muscular system, and this is correlated with the movement necessary for the head in burrowing.

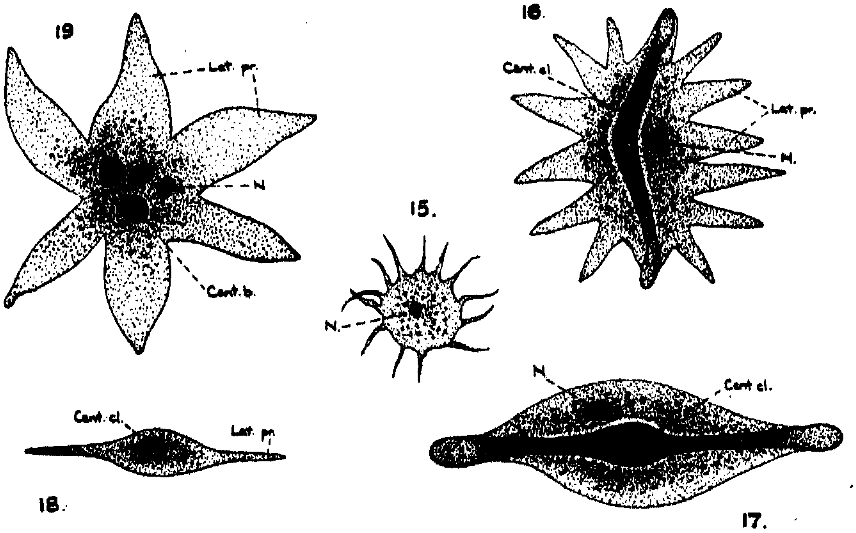
The body cavity is undivided by septa, except in the anterior region where there are two, at the hind ends of segments 2 and 3. They form a conical cæcum which projects backwards dorsal to the œsophagus, one septum being inside the other (fig. 25, *Caec.*). (One specimen showed two conical sacs, each formed by the backward projection of both septa in two places, lying side by side above the œsophagus.) The presence of this organ in other species of *Ophelia* has been the cause of much discussion by early workers, and it has been described at different times as a respiratory vesicle, a salivary gland, a fleshy heart, and a digging organ. De Quatrefages (1865) considered it to be an exsertile funnel, but Claparède (1868) has described it as an injector organ, the contraction of which, by increasing the turgidity of the body in front of the cæcum, stiffens the cephalic region of the animal, and is thus an aid in burrowing. In this view he is supported by Pruvot (1885) and de Saint-Joseph (1898). Unfortunately, it is difficult to observe any contractions of the cæcum through the body wall, but these doubtless take place, as both septa forming the cæcum have a well-developed muscular coat. This conical cæcum is probably homologous, as de Saint-Joseph (1898) has said, with the œsophageal diaphragm of Terebellids. A similar, though much smaller, organ has been described by Ashworth (1904) in *Arenicola.*

Cœlome and Cœlomic Fluid.—The cœlome is spacious, especially in the anterior swollen part of the body, and is continuous from side to side and from end to end of the animal, except where it is interrupted by the septa mentioned above.

The cœlomic fluid contains the reproductive cells in various stages of development. Also suspended in the fluid is a large number of lymphatic corpuscles, two kinds of which are readily distinguishable. Those of the first type are small discoid cells, commonly about 15–20 μ in diameter, the periphery of which has a frill formed by narrow processes (fig. 15). Their ectoplasm is clear, and their endoplasm is of a granular nature, enclosing a central nucleus. Those of the second type are characterised by their possession of a dark-brown solid inclusion, occasionally in the form of two or three spherical bodies (fig. 19), but generally rod- or club-shaped (figs. 16, 17, 18). Typical rod-cells may be found in the body-fluid varying in size from 40 to 150 μ. They are elongated, and, like the simple corpuscles, the endoplasm is granular, while the clear ectoplasm may form radial processes, often difficult to distinguish. The nucleus is usually opposite the middle of the club.

Schaeppi (1894), who has studied these corpuscles in *O. radiata*, describes the development of the rod-cells from the simple discoid type, and shows that the rod is formed by the aggregation of chloragogen granules which are formed in the cell.

The cœlomic fluid is almost continuously in motion, even when the animal is at rest, owing to the movement of the stomach, which is constantly being jerked backwards and forwards during life.



FIGS. 15–19.—Lymphatic corpuscles. *Cent. b.*, central body of the lymphatic corpuscle; *Cent. cl.*, axial club; *Lat. pr.*, lateral processes; *N.*, nucleus.

FIG. 15.—"Radial" type. (×650.)
FIGS. 16 and 17.—Common "club" types. (×470.)
FIG. 18.—End view of "club" type. (×460.)
FIG. 19.—Exceptional type. (×730.)

Alimentary Canal.—The mouth opens on the ventral side at the posterior extremity of the first segment. It leads by a short tube, running dorsally, and flattened antero-posteriorly, into the proboscis or eversible portion of the buccal region. This portion lies dorsal to the mouth and can be seen on dissection to be retracted into a much convoluted mass, with two main longitudinal and many smaller longitudinal and lateral folds (fig. 25, *Prob.*). This proboscis can, on relaxation of its retractor muscles, be blown out by contraction of the muscles of the body-wall, and this may be helped by contraction of the muscles of the injector organ. When exserted, the proboscis has a button-shaped appearance (fig. 3, *Prob.*), and the ventral and internal portion of it is ciliated (*Prob. cil.*). When feeding, the everted proboscis engulfs one or two sand-grains, together with any food particles in their vicinity, and is then withdrawn.

The proboscis is followed by a short œsophagus (fig. 25, *Oes.*), the wall of which is slightly convoluted (fig. 20), but a peri-œsophageal blood sinus such as has been described by de Saint-Joseph (1898) in *O. neglecta* does not occur in this species.

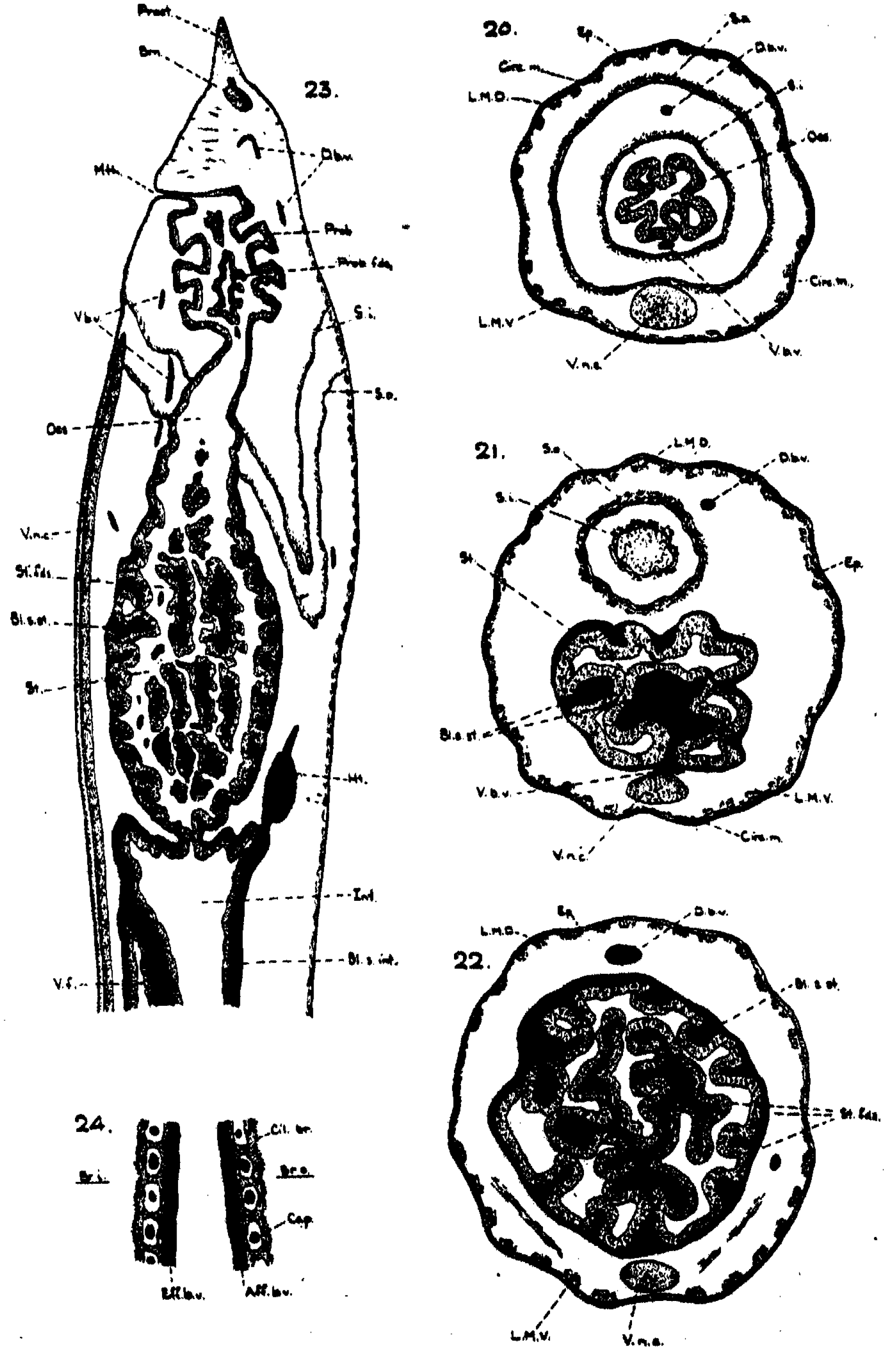
The œsophagus leads into the wider stomach, the walls of which are thrown into a complicated series of folds. A large blood sinus surrounds the stomach, the blood filling the spaces between the folds. These folds, as may be seen in transverse section (fig. 22, *St. fds.*), are not confined to the outer surface of the stomach, for a large ventral fold gives rise to a further series of internal secondary folds, almost completely filling the interior of the stomach. It is obvious that the stomach is not constructed in this way to allow of expansion when filled with sand, for the periphery of the stomach is greater than that of the body-wall itself. Furthermore, the membrane which surrounds the peristomachal sinus allows little margin for general expansion. It seems probable, therefore, as is thought by Schaeppi (1894), that the importance of these folds lies in the fact that they increase the surface of the stomach wall which is brought into contact with the blood in the sinus, forming an alimentary respiratory system.

The stomach has a slight loop when the animal is moving about in the sand, and this permits the swinging movement of the alimentary canal, which goes on vigorously and almost continuously. A similar movement is described in other limivorous forms, notably by Ashworth in *Arenicola* (1904) and *Scalibregma* (1901).

The stomach is constricted at its posterior end (fig. 23), and passes over into the intestine at about the level of the ninth pair of chætæ. The intestine is narrower than the widest part of the stomach, and is not thrown into sinuous folds like the latter. A ventral fold is still present, and fairly extensive (fig. 9, *V.f.*), but no secondary folds occur. The intestine is surrounded by a blood sinus, which is more capacious than the peristomachal blood sinus. The intestine continues backward to the anus without change in character.

Blood System.—The blood, as in other members of the Opheliidæ, is red, due to hæmoglobin dissolved in the plasma. Scattered throughout the blood there is a number of blood corpuscles. They are about 7–9 μ in size, roughly spherical or slightly ovoid in shape, sometimes with short radial processes, and possess a large nucleus. They are comparatively few in number, and their function is unknown.

The great sinuses which surround the stomach and intestine have already been mentioned. Their walls are thin, but the wall of the intestinal blood sinus becomes thicker towards its posterior end. At the



FIGS. 20–24.—*Aff. b. v.*, afferent branchial vessel; *Bl. s. int.*, intestinal blood sinus; *Bl. s. st.*, stomachal blood sinus; *Br. i.*, *Br. o.*, inner and outer sides of gill; *Brn.*, brain; *Cap.*, capillary; *Cil. br.*, cilia of gill; *Circ. m.*, circular muscle; *D.b.v.*, dorsal blood-vessel; *Eff. b. v.*, efferent branchial vessel; *Ep.*, epidermis; *Ht.*, heart; *Int.*, intestine;

anterior end of the intestinal blood sinus, on the dorsal side, a large blood-vessel is given off, and this runs forward almost immediately into the heart (fig. 25, *Ht.*). The heart lies dorsal to the posterior end of the stomach, and is simply a swollen part of the dorsal blood-vessel; indeed, when seen in systole, there is little to differentiate it from the rest of the dorsal vessel.

Immediately in front of the heart, the dorsal vessel gives off a branch on each side, which travels round the stomach in a ventero-posterior direction to the ventral side of the alimentary canal at the junction of the stomach and intestine, where it unites with its fellow to form the posterior ventral vessel. Like the dorsal vessel, these branches are contractile. They give off a number of small vessels to the ventral body wall and muscles, and also to the seventh and eighth chæta-sacs. The dorsal vessel also gives rise to another pair of lateral vessels which pass round the anterior end of the stomach. These give rise to smaller vessels which supply the sixth chæta-sacs. Farther forward, two more pairs of lateral vessels can be seen, and these go directly to the fourth and fifth chæta-sacs.

The dorsal vessel then runs forward through the two septa and emerges on the dorsal side of the retracted proboscis. It goes forward almost as far as the brain, bends back on itself, and travels ventrally towards the mouth. In this region it splits into two side trunks, much reduced in size, and these supply the proboscis.

The anterior ventral vessel arises behind the mouth and beneath the proboscis, and runs backwards, receiving a few vessels from the body-wall, finally disappearing into the peristomachal blood sinus.

The posterior ventral vessel originates at the anterior end of the intestine, and is formed by the fusion of the two branches from the dorsal vessel just anterior to the heart. It runs backwards, giving off on each side a small branch to each chæta-sac. An afferent branchial vessel supplies each gill, together with the nephridium where present, and an efferent branchial vessel returns from the gill to the intestinal blood sinus.

The stomachal blood sinus gives off a few vessels to the dorsal and ventral body-wall. All the vessels going to the body wall are long and

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L.M.D., dorsal longitudinal muscle; *L.M.V.*, ventral longitudinal muscle; *Mth.*, mouth; *Oes.*, œsophagus; *Prob.*, proboscis; *Prob. fds.*, folds of proboscis; *Prost.*, prostomium; *S.i.*, *S.o.*, inner and outer sacs of injector organ; *St.*, stomach; *St. fds.*, stomach folds; *V.b.v.*, ventral blood-vessel; *V.f.*, ventral fold of intestine; *V.n.c.*, ventral nerve cord.

FIG. 20.—T.S. of worm through segment 4. (× 32.)
FIG. 21.—T.S. at anterior end of stomach. (× 32.)
FIG. 22.—T.S. at posterior end of stomach. (× 32.)
FIG. 23.—Median longitudinal section through the anterior end of the worm (semi-diagrammatic). (× 25.)
FIG. 24.—Section through a gill at right angles to axis of body. (× 315.)

often looped, so as to allow the alimentary canal to swing freely in the cœlome.

Gills.—The gills are small, tapering hollow tubes which arise from the latero-ventral folds of the body, dorsal to the chætæ. They are about 0·7 mm. long, and are very slightly ringed transversely, giving a scarcely perceptible hooped appearance. In life they are red, due to their abundant blood-supply. They are seen in section (fig. 24) to be constructed in a basket-like fashion, with a series of cubical spaces around the periphery. The whole surface of the gill is ciliated, and a current of fresh sea-water is thus made to pass continuously over the gill.

Each gill is supplied by an afferent vessel (*Aff.b.v.*) arising from the ventral blood-vessel. It enters on the outer side of the gill, keeping close to the basket-work and running up to the tip. In its progress it breaks up into fine branches, which run transversely round the gill in the middle of the cubical spaces. These capillaries collect again on the inner side of the gill and form an efferent branchial vessel (*Eff.b.v.*), which leaves the gill and opens into the intestinal blood sinus.

Nervous System.—The cerebral mass is situated partly in the prostomium and partly in the anterior portion of the first body segment. It is very small, being only 0·2 mm. broad. It is roughly square in shape as seen from above (fig. 29), with a small lobe at each side of its posterior end. It is orientated in such a manner that its anterior is lower than its posterior end, and is thus seen from the side to be sloping at an angle of about 45° (fig. 28). It has two dorso-lateral lobes (*Nuc. Tr.*) which abut on the inner side of the nuchal organs, and two anterior lobes (*L. ant.*) which run forward into the prostomium. As Pruvot (1885) points out, these are not nerves, but actually prolongations of the cerebral mass. Sections of the brain show it to be composed of two regions, an anterodorsal densely nucleated part and a postero-ventral non-nucleated part.

The eyes are embedded in the substance of the brain. There is a right and left eye placed anteriorly (*E. ant.*), and a single posterior eye (*E. post.*) situated just in front of the left posterior lobe of the brain. The eyes are slightly flattened spheres about 20 μ in diameter. They consist of a lens surrounded by a large number of closely aggregated dark-brown pigmented granules. The pigment dissolves out when left for a long time in alcohol.

The œsophageal connectives (fig. 28, *Oes. comm.*) arise from the ventral side of the brain, and pass backwards towards the mouth along the ridges forming the boundaries of the triangular areas in the mouth region. These ridges are seen from the exterior as grooves. The connectives are small and flat where they leave the brain, but they enlarge slowly on their

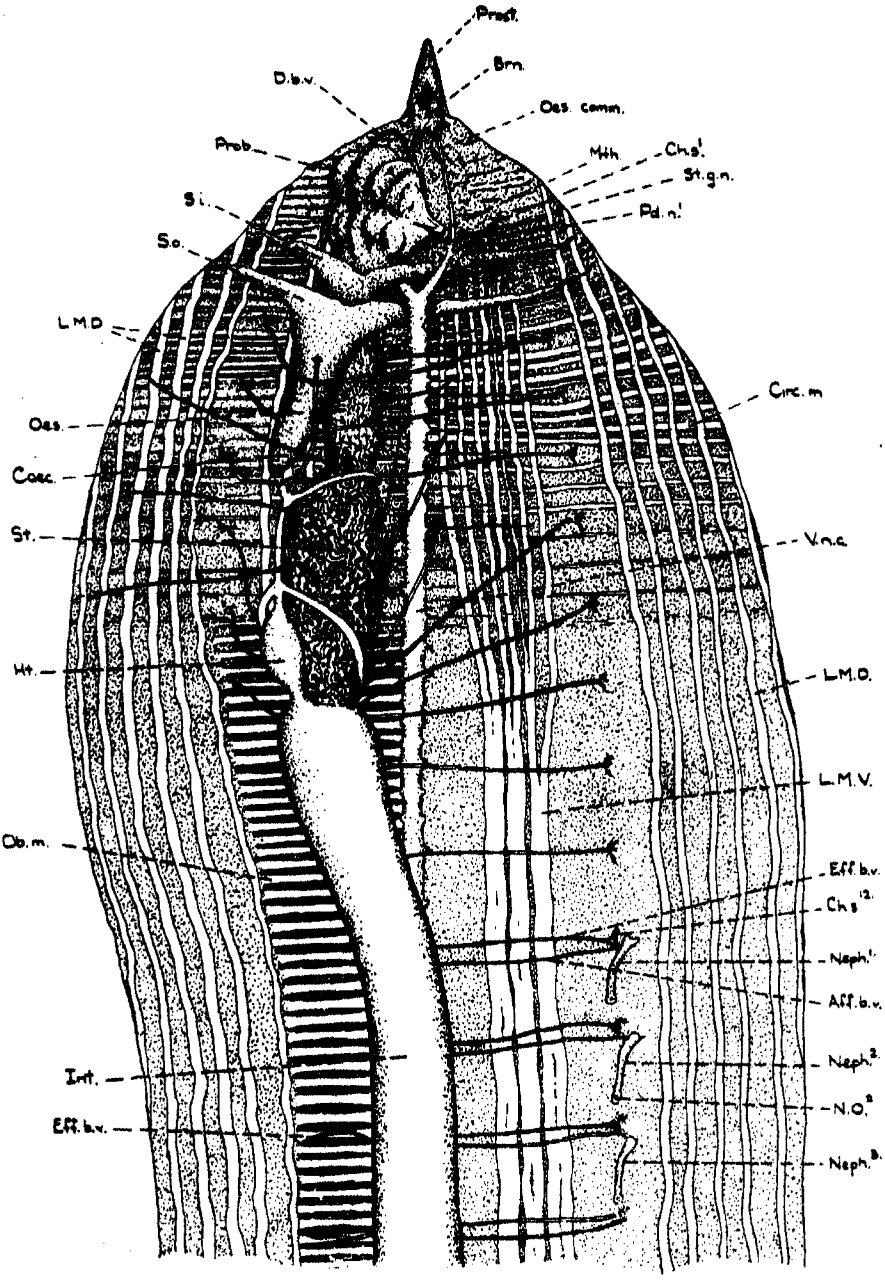


FIG. 25.—Anterior end of a specimen opened by means of a mid-dorsal cut. (× 14·8.) The alimentary canal has been pushed to one side and the oblique muscles on the right side have been removed to show the nephridia, etc.

Aff. b.v., afferent branchial vessel; *Brn.*, brain; *Caec.*, injector organ; *Ch.s.*^{1}, *Ch.s.*^{12}, first and twelfth chæta-sacs; *Circ. m.*, circular muscle; *D.b.v.*, dorsal blood-vessel; *Eff. b. v.*, efferent branchial vessel; *Ht.*, heart; *Int.*, intestine; *L.M.D.*, dorsal longitudinal muscle; *Mth.*, mouth; *Neph.*^{1}–*Neph.*^{3}, the three nephridia; *N.O.*^{2}, second nephridial opening; *Ob. m.*, oblique muscle; *Oes.*, œsophagus; *Oes. comm.*, œsophageal commissures; *Pd. n.*^{1}, first pedal nerve; *Prob.*, proboscis; *Prost.*, prostomium; *S.i.*, *S.o.*, inner and outer sacs of injector organ; *St.*, stomach; *St. g. n.*, stomato-gastric nerve; *V.n.c.*, ventral nerve cord.

way backwards, until they meet behind the mouth, where they become slightly swollen out before joining the ventral nerve cord (fig. 25). Just before they meet the ventral nerve cord they pass through the anterior septum which forms the inner sac of the injector organ, so that the actual junction takes place in the middle of the third body segment.

Opposite the mouth, each œsophageal commissure gives off a small branch (fig. 25, *St.g.n.*) which runs along the ventral body-wall and up the side of the tube leading into the proboscis; this is the stomato-gastric nerve. The first pedal nerves are given off on each side just in front of the junction with the ventral nerve chain (fig. 25, *Pd.n.*[1]). These supply the first pair of chæta-sacs.

The ventral nerve cord passes back through the second septum and along the mid-ventral line almost to the anus. It is a thick band, slightly flattened dorso-ventrally, and its edges are almost parallel—that is, there is no obvious aggregation into ganglia. In transverse section (fig. 30), the cord is seen to have three nuclear groups—a central (*Gr. nu. med.*) and two lateral (*Gr. nu. lat.*). The histology of the central nervous system of Opheliids has been studied by Kükenthal (1887).

The ventral nerve cord gives off a small nerve to each chæta-sac, and others to the body-wall and muscles.

The prostomium and the nuchal organs are the principal sense organs. The prostomium, supplied directly from the brain, is very rich in sensory cells. The nuchal organs are situated above the brain and are also innervated directly from it. They are pocket-like structures, forming a groove externally—the nuchal groove (fig. 7, *Nuc. gr.*). The organ is capable of evagination, when it forms a flattened bulb, elongated dorso-ventrally, and covered with cilia (fig. 8, *Nuc. org.*). It has a mass of columnar sensory cells (fig. 14) abutting on its internal surface, in communication with the brain.

There is no trace in *O. cluthensis* of the sensory pits between the notopodial and neuropodial chætæ found in other species of *Ophelia*, nor is there any sign of sensory hairs. Sense cells may be present, however, among the thick mass of cells between the bases of the two groups of chætæ.

Nephridia (figs. 26, 27).—There are three pairs of nephridia, situated on segments 13, 14 and 15. They lie close to the body-wall in the latero-ventral folds, and may be seen on microscopical examination of live specimens as small whitish areas.

The nephridiopores (*N.O.*) can be readily seen as they are situated on papillæ just in front of the parapodia. Each nephridium is a simple tube extending from the nephridiopore forwards and upwards, increasing steadily in diameter, and opening to the interior by a wide-mouthed nephrostome (*Nephst.*) opposite the gill in front. The tube is ciliated throughout, and is about 14 μ in diameter in its distal portion. The nephridia are supplied by a branch of the afferent branchial vessel.

Gonads.—The reproductive cells in different stages of development are found in all parts of the cœlome, and they are especially closely packed in the latero-ventral folds, beneath the oblique muscles.

So far as is known, gonads have not been described in any species of *Ophelia*, and no specialised organs were found in this species. The reproductive cells are proliferated mainly from the cœlomic epithelium covering the blood-vessels supplying the gills in each of the gill-bearing segments. In addition they have been found on the cœlomic epithelium covering the third pair of nephridia, and, since proliferation from the blood-vessels takes place in the same relative position as the nephridia, this may be regarded as evidence of an ancestral series of "segmental organs." The reproductive cells are shed into the cœlome at an early stage, and there complete development.

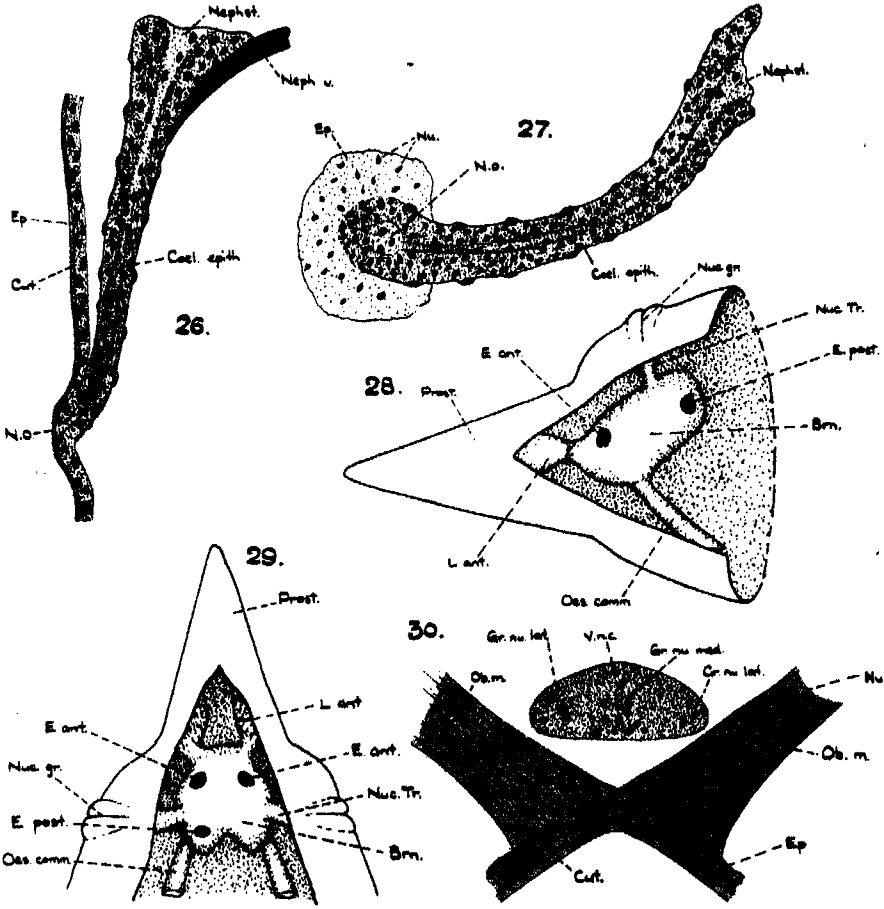
The ripe eggs are white discs, their flattened surface being almost circular in outline (fig. 31). They are about 0·14–0·15 mm. in diameter, and about 0·05–0·06 mm. thick. The egg is surrounded by a membrane of about 5 μ in thickness, and the large vesicular nucleus, showing very dark in life, gives the egg the appearance of being ring-shaped. A dark nucleolus is eccentrically placed in the nucleus.

The heads of the ripe spermatozoa are hat-shaped (fig. 32), and measure about 5·5 μ across the "brim," above which the tail originates. The tail measures about 45 μ in length. The nucleus, only visible when stained, occupies almost the whole of the rounded end of the spermatozoon.

Ophelia cluthensis has two broods in the year—in April and September, and eggs laid in April produce small worms of 2 mm. length by June (McGuire, 1935).

I have never seen the worms spawning, and how the eggs and sperms are passed to the exterior I am unable to say. It is obvious that the eggs cannot escape by the nephridia owing to their larger size, and while the sperms could certainly traverse the nephridial tubes they could only do so singly. It seems probable, as has been observed in some other families, that the ova and spermatozoa are shed by local rupture of the body-wall. According to Benham (1901) the eggs of other species of *Ophelia* are laid in a jelly.

I have tried to fertilise ova taken from the body cavity of apparently ripe females with active spermatozoa from a ripe male. The spermatozoa in many cases attached themselves to the eggs by the flattened part of their head (fig. 33), but I have been unable to obtain any division stages. McGuire (1935), however, obtained fertilised eggs and observed cell division up to the four-cell stage.

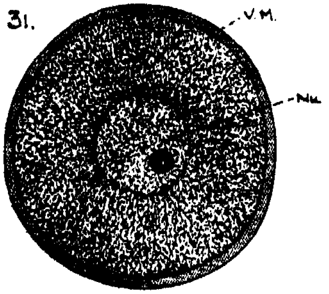


FIGS. 26–30.—*Brn.*, brain; *Coel. epith.*, cœlomic epithelium; *Cut.*, cuticle; *E. ant.*, *E. post.*, anterior and posterior eyes; *Ep.*, epidermis; *Gr. nu. lat.*, *Gr. nu. med.*, lateral and median nuclear groups; *L. ant.*, anterior lobe of brain; *Nephst.*, nephrostome; *Neph. v.*, nephridial blood-vessel; *N.O.*, nephridial opening; *Nu.*, nucleus; *Nuc. gr.*, nuchal groove; *Nuc. tr.*, nuchal lobe; *Ob. m.*, oblique muscle; *Oes. comm.*, œsophageal commissures; *Prost.*, prostomium; *V.n.c.*, ventral nerve cord.

FIG. 26.—Nephridium viewed in optical section from the dorsal side. (× 80.)
FIG. 27.—Nephridium viewed in optical section from the side. (× 80.)
FIG. 28.—Dissection of head end from side to show the brain. (× 80.)
FIG. 29.—Dissection of head end from above. (× 80.)
FIG. 30.—T.S. through the ventral region in the middle of the body. (× 165.)

Bullot (1904) has been able to induce artificial parthenogenesis in eggs of an unnamed species of *Ophelia* by placing them for a time in potassium chloride and then back into sea-water. In this way he was able to obtain a small percentage of swimming blastulæ, superficially similar to those produced by ordinary fertilisation. I have tried this method with eggs of *O. cluthensis*, but again, unfortunately, without success. In both cases, failure has probably been due to my inability to obtain eggs which were quite ripe.

31.



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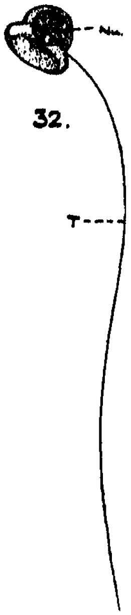
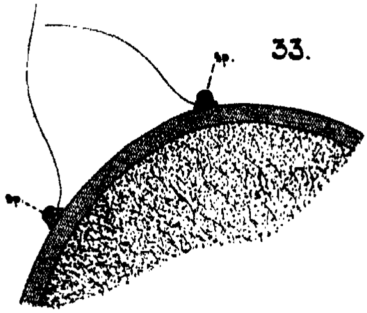


33.



Figs. 31–33.—*Nu.*, nucleus; *Sp.*, spermatozoon; *T.*, tail of spermatozoon; *V.M.*, vitelline membrane.

Fig. 31.—Egg viewed on flattened surface (from a stained specimen.) (×250.)

Fig. 32.—Spermatozoon. (×1700.)

Fig. 33.—Portion of egg with spermatozoon attached, before fertilisation. (×510.)

The larval stages, therefore, beyond the four-cell stage are as yet unknown.

AFFINITIES.

In the family Opheliidæ, the genus *Ophelia* is distinguished by the fact that the ventral groove is confined to the posterior part of the body. Fauvel (1927) describes four species—*O. bicornis* Savigny, *O. radiata* Delle Chiaje, *O. neglecta* Schneider, and *O. limacina* Rathke. The first three are similar in many respects, but *O. limacina* is distinctive in having a few (2–4) large pad-like structures on the posterior part of the body. Of the others, all have 32 setigerous segments, but differ from one another in the number of gills and in the number of anal papillæ, although the latter number is in all three species very variable. *O. cluthensis* differs from all four species in possessing only 24 setigerous segments and 8–10 pairs of gills, the smallest number of gills in the other species being 14—in *O. radiata.* It differs also in the number of nephridia. While it possesses only three pairs of nephridia, opening on segments 13–15, the other species have six, opening on segments 12–17.

It resembles *O. bicornis* in having no anal valve in the rectum, but is again marked off from the other species by its possession of only one large ventral anal papilla, all the others having two.

Another point of difference is in the number of eyes. These are completely absent in *O. bicornis* (Pruvot, 1885). The two anterior eyes are present in *O. radiata* according to Claparède (1868), while according to de Saint-Joseph (1898), in *O. neglecta* the two anterior and the left posterior eyes are evident, while the right posterior is degenerate and visible only as a few granules of pigment. *O. cluthensis*, as has been described, possesses three eyes, the two anterior and the left posterior. Fauvel (1927), however, does not regard the eyes as being important diagnostic features, on account of the fact that they discolour after a time in alcohol, and have, therefore, been the subject of some controversy.

Ophelia cluthensis is thus markedly distinct from the other species of the genus, and it is difficult to relate to any one of these species. Whether it is a more primitive, degenerate or more specialised form is not yet clear, but it is possible that a fuller investigation involving a study of the life-history will settle this point.

I am indebted to Professor Edward Hindle of the Zoology Department of Glasgow University for the helpful advice and suggestions he has given during the course of this work.

To Mr Richard Elmhirst, Director of Millport Marine Biological Station, I am grateful for an abundant supply of material, and for information on many points, including the data of a survey of the distribution of *Ophelia cluthensis* in Kames Bay, Millport.

I have to thank Dr A. C. Stephen of the Royal Scottish Museum, Edinburgh, who has kindly given me records in his possession of the occurrence of this species, and also for his figures, giving the zonation of the worm in Kames Bay and in Fairlie Sands, which have been included in this paper.

My thanks are also due to Mr Alexander McKinnon, technician in the Zoology Department of Glasgow University, for suggestions regarding section-cutting, and to Mr J. W. Morton, who assisted me in making counts of the worms at Millport.

SUMMARY.

This paper describes the anatomy of the Polychæte worm *Ophelia cluthensis*, which is found in the sand just below High Water Neap tides.

An account is given of its distribution on the shore at Kames Bay, Millport, together with the results obtained from counts of the worms made there and in Fairlie Sands.

O. cluthensis is 9·5 mm. to 18 mm. in length, the male being slightly smaller than the female. It has 25 segments, the first 24 of which are setigerous, and 8–10 pairs of gills borne on segments 12–13 to 20–21. The posterior ventral furrow and latero-ventral folds characteristic of the genus begin between segments 8 and 9. The anal segment is achætous, and the anus is surrounded by 12 papillæ—one small dorsal, one large ventral, and 5 pairs of lateral. Three pairs of nephridia open laterally on small papillæ on segments 13–15. The brain bears three eyes embedded in its substance, visible through the body-wall as black specks.

The affinities of the species with other members of the genus are discussed.

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DESCRIPTION OF PLATE.

FIG. A.—*Ophelia cluthensis.* Dorsal view of a fully expanded specimen. (× 11.)

The heart and the dorsal blood-vessel with its branches can be seen through the body-wall, and these, together with the hinder region of the body and the gills, are red in the live specimen from the contained blood. The stomach shows as a dark patch.

FIG. B.—Ventral view of the same specimen. (× 11.)

The ventral nerve cord and œsophageal commissures can be seen through the body-wall, and the ventral attachments of the oblique muscles show in the ventral groove as white areas between dark transverse lines on each side of the ventral nerve cord.

An., anus; *An. pap.*, anal papillæ; *Br.*^{1}, *Br.*^{9}, first and ninth gills; *Brn.*, Brain; *D.b.v.*, dorsal blood-vessel; *Ht.*, heart; *L.v.f.*, latero-ventral fold of body; *Mth.*, mouth; *N.O.*^{1}–*N.O.*^{3}, nephridial openings; *Nuc. org.*, nuchal organ; *Oes. comm.*, œsophageal commissure; *Ppm.*^{1}, *Ppm.*^{24}, first and twenty-fourth parapodia; *Prost.*, prostomium; *St.*, stomach; *V.b.v.*, ventral blood-vessel; *V.gr.*, ventral groove; *V.n.c.*, ventral nerve cord.

(*Issued separately June* 9, 1938.)

Fig. A.

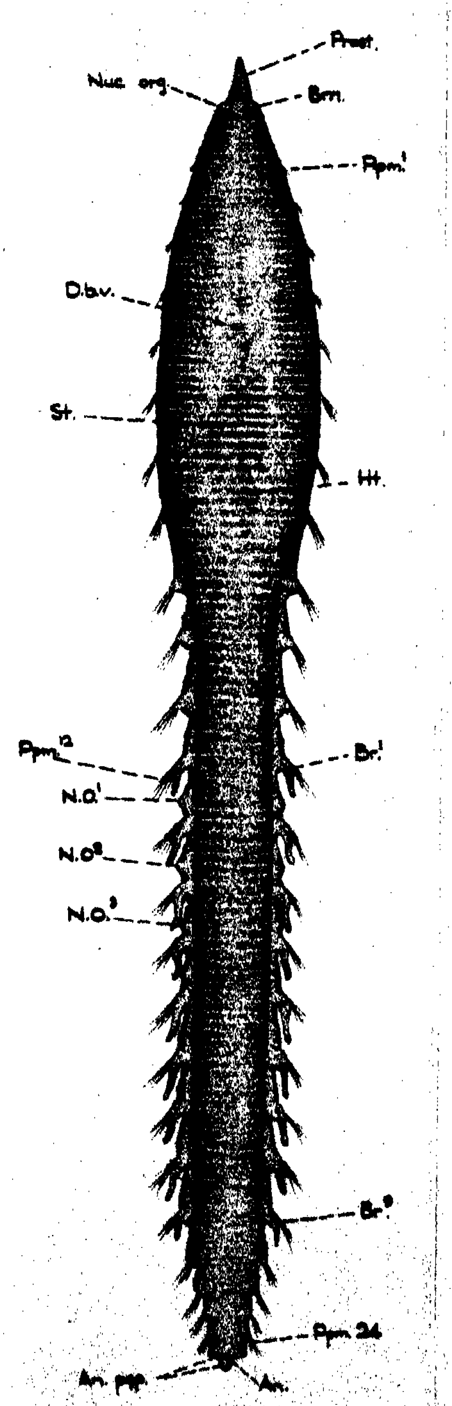
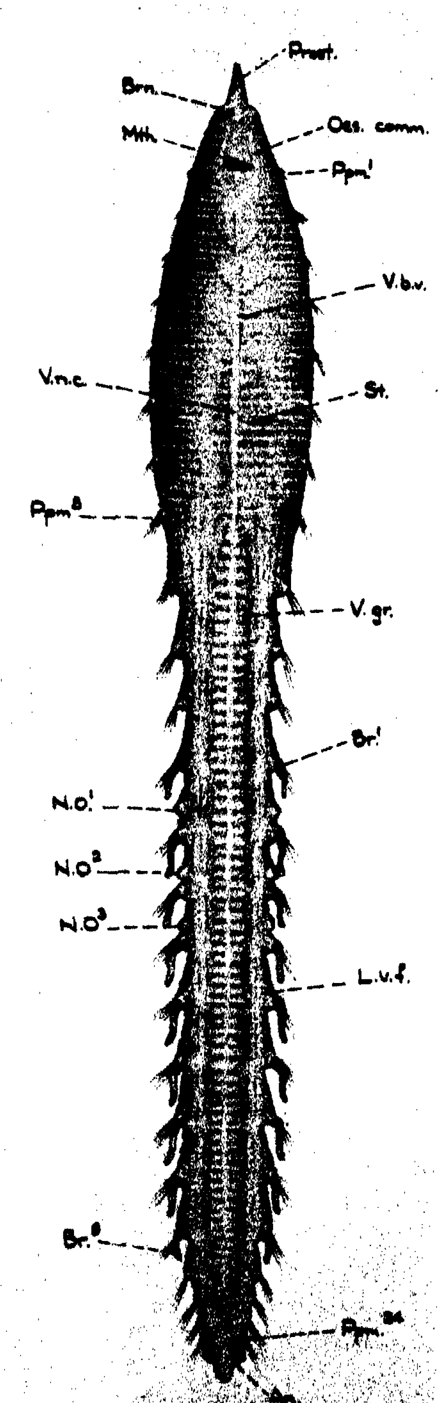


Fig. B.



R. S. Brown.

XI.—Studies in Practical Mathematics. III. The Application of Quadratic Extrapolation to the Evaluation of Derivatives, and to Inverse Interpolation.

By **A. C. Aitken**, D.Sc., F.R.S., Mathematical Institute, University of Edinburgh.

(MS. received January 17, 1938. Read March 7, 1938.)

1. INTRODUCTORY.

IN an earlier paper (Aitken, 1932) the author put forward a method of polynomial interpolation which was designed to make full use of the speed and power of modern calculating machines in forming and summing products of two factors. The present paper is devoted to two further applications of the method. It is necessary to give a brief review and explanation of the process used, in order that these applications may be properly understood.

The problem investigated in the earlier paper was the standard one of finding by polynomial interpolation the value of u_x, given tabular values u_a, u_{-a}, u_b, u_{-b}, u_c, u_{-c}, . . . symmetrically disposed in pairs about a central value u_0, which may or may not appear in the table. Most frequently, when the function u is tabled at equal intervals of its argument, the "central panel" is from $u_{-\frac{1}{2}}$ to $u_{\frac{1}{2}}$ and the values of a, b, c, . . . are 1/2, 3/2, 5/2, . . ., but sometimes, when the central value u_0 appears in the table but is not used in the interpolation, the central panel is from u_{-1} to u_1 and the values of a, b, c, . . . are 1, 2, 3, . . . The method of interpolation proposed was as follows:—

(i) Interpolate linearly for u_x between the symmetrically placed pairs of tabular values u_a, u_{-a}; u_b, u_{-b}; u_c, u_{-c}; and so on, obtaining "linear cross-means" (Lidstone, 1937, p. 274):

$$u_{a,-a} \equiv u_{\pm a} = \{(a-x)u_{-a} + (a+x)u_a\}/2a, \quad . \quad . \quad . \quad (1)$$

$u_{\pm b}$, $u_{\pm c}$, and so on. These cross-means, which are even functions of their arguments a, b, c, . . ., are the basis of further interpolation, carried out in the manner now to be described.

(ii) Form from these linear cross-means a sequence of "quadratic cross-means," as follows:—

$$u_{\pm a,\pm b} = \{\tfrac{1}{2}(b^2-x^2)u_{\pm a} - \tfrac{1}{2}(a^2-x^2)u_{\pm b}\}/\tfrac{1}{2}(b^2-a^2), \quad . \quad . \quad (2)$$

$u_{\pm a, \pm c}$, $u_{\pm a, \pm d}$, and so on. Continue with

$$u_{\pm a, \pm b, \pm c} = \{\tfrac{1}{2}(c^2 - x^2)u_{\pm a, \pm b} - \tfrac{1}{2}(b^2 - x^2)u_{\pm a, \pm c}\}/\tfrac{1}{2}(c^2 - b^2), \quad . \quad (3)$$

$u_{\pm a, \pm b, \pm d}$, and so on. The quadratic cross-means of successive order obtained in this way are set out in a working scheme of successive columns, the quadratic multipliers being given in a column on the extreme right; the scheme is described in full detail in the former paper, and will be seen in operation in the examples of §§ 2, 3, 4 below. The convergence of the interpolation is indicated to the eye of the computer by the convergence towards equality of consecutive cross-means in the same column at any stage; the process is stopped at the stage when such entries agree to an assigned number of digits.

The features which make the construction of quadratic cross-means a simple and rapid computing process are these:

(i) In the commonly occurring practical case of functions tabled at equal intervals of x, where $a, b, c, \ldots$ are either $1/2, 3/2, 5/2, \ldots$ or $1, 2, 3, \ldots$, all quadratic multipliers have the same decimal part, which need be recorded in full once only on the computing sheet, and can be left on the setting levers of the machine through the whole of the computation.

(ii) The differences of the quadratic multipliers, which constitute the divisors used in forming cross-means, are convenient small integers. Here we must observe that in our former paper we took the multipliers in the numerators of the cross-means invariably as $a^2 - x^2$, $b^2 - x^2$, . . .; further experience has shown that though this is useful in the less common case when $a, b, c, \ldots$ are $1, 2, 3, \ldots$, it is better when $a, b, c, \ldots$ are halves of odd integers to take $(a^2 - x^2)/2$, $(b^2 - x^2)/2$, . . . as multipliers, for then the divisors are the smaller and more convenient numbers 1, 3, 6, 10, . . .; 2, 5, 9, . . .; 3, 7, 12, . . .; and so on.

In the theoretical discussion it is better to preserve symmetry, and to centre the data about the "central panel" $u_{-\frac{1}{2}}$, $u_{\frac{1}{2}}$. In the practical description, however, it is better to name the central panel u_0, u_1, as in the usual text-book presentation of Everett's formula. To show how the cross-means are computed in practice we may take a simple illustration, the evaluation of $u_{0\cdot 74}$ from . . . u_{-2}, u_{-1}, u_0, u_1, u_2, . . . The linear cross-means would then be

$$\begin{aligned} u_{0,1} &= 0{\cdot}74u_1 + 0{\cdot}26u_0, \\ u_{-1,2} &= (1{\cdot}74u_2 + 1{\cdot}26u_0)/3, \\ u_{-2,3} &= (2{\cdot}74u_3 + 2{\cdot}26u_0)/5, \end{aligned}$$

and so on. The first column of quadratic cross-means, all constructed with multipliers having decimal part 0·74(1 − 0·74)/2 or 0·0962, would be

$$\begin{aligned} u_{-1,0,1,2} &= 1{\cdot}0962u_{0,1} - 0{\cdot}0962u_{-1,2}, \\ u_{-2,0,1,3} &= (3{\cdot}0962u_{0,1} - 0{\cdot}0962u_{-2,3})/3, \\ u_{-3,0,1,4} &= (6{\cdot}0962u_{0,1} - 0{\cdot}0962u_{-3,4})/6, \end{aligned}$$

and so on. These in their turn would yield the next column,

$$\begin{aligned} u_{-2,-1,0,1,2,3} &= (3{\cdot}0962u_{-1,0,1,2} - 1{\cdot}0962u_{-2,0,1,3})/2, \\ u_{-3,-1,0,1,2,4} &= (6{\cdot}0962u_{-1,0,1,2} - 1{\cdot}0962u_{-3,0,1,4})/5, \end{aligned}$$

and so on. These again would yield

$$u_{-3,-2,1,0,1,2,3,4} = (6{\cdot}0962u_{-2,-1,0,1,2,3} - 3{\cdot}0962u_{-3,-1,0,1,2,4})/3,$$

and so on. The entries in the column reached at this stage contain approximations to u_x based on polynomials of the seventh degree determined by eight tabular values, as indicated by the suffixes. To compute any cross-mean is the matter of a few seconds; and in the later stages, when cross-means in the same column converge to agreement in their more important digits, we need form cross-means of the later and differing digits only, since those digits which are common to both will be reproduced under the operation of weighted mean, and therefore need be recorded in the first entry only of any column. (See again the example of § 2 below.)

With these necessary preliminaries, we now proceed to show how, by adding to the cross-products certain easily computed terms, we may evaluate $u_x, u_x', u_x'', u_x''', \ldots$ and, indeed, any further number of derivatives of consecutive orders.

2. COMPUTATION OF DERIVATIVES BY QUADRATIC CROSS-MEANS.

Let a cross-mean, such as appears in § 1 (3), be differentiated n times by Leibniz's Theorem. We obtain

$$u^{(n)}_{\pm a, \pm b, \pm c} = \frac{\frac{1}{2}(c^2 - x^2)u^{(n)}_{\pm a, \pm b} - \frac{1}{2}(b^2 - x^2)u^{(n)}_{\pm a, \pm c} + nx\{u^{(n-1)}_{\pm a, \pm c} - u^{(n-1)}_{\pm a, \pm b}\} + n_{(2)}\{u^{(n-2)}_{\pm a, \pm c} - u^{(n-2)}_{\pm a, \pm b}\}}{\frac{1}{2}(c^2 - b^2)}, \qquad (1)$$

where $n_{(2)} = n(n-1)/2$. The corresponding result for a quadratic cross-mean of any order is of similar form. Hence, provided we have suitable values to insert in the first columns of the computation, we may form derivatives by constructing cross-means; it is only necessary to add to the cross-product, before it is divided by $(c^2 - b^2)/2$ or the like, the terms

$$nx\{u^{(n-1)}_{\pm a, \pm c} - u^{(n-1)}_{\pm a, \pm b}\} + n_{(2)}\{u^{(n-2)}_{\pm a, \pm c} - u^{(n-2)}_{\pm a, \pm b}\}. \qquad . \qquad . \qquad (2)$$

The terms in brackets here are simple differences of entries which will already have been used in evaluating earlier derivatives $u_x^{(n-1)}$ and $u_x^{(n-2)}$.

In this way the computation of any derivative supplies certain columns of differences which are used for computing the next two derivatives. For the first derivative we have $n=1$, the added terms taking the simple form

$$x\{u_{\pm a,\,\pm c}-u_{\pm a,\,\pm b}\}, \quad . \quad . \quad . \quad . \quad . \qquad (3)$$

involving differences of cross-means appearing in the calculation of u_x. For the second derivative the added terms are

$$2x\{u'_{\pm a,\,\pm c}-u'_{\pm a,\,\pm b}\}+\{u_{\pm a,\,\pm c}-u_{\pm a,\,\pm b}\}. \quad . \quad . \quad . \qquad (4)$$

For the third derivative they are

$$3x(u''_{\pm a,\,\pm c}-u''_{\pm a,\,\pm b})+3(u'_{\pm a,\,\pm c}-u'_{\pm a,\,\pm b}), \quad . \quad . \quad . \qquad (5)$$

and so on. To begin the process, we merely note the initial values

$$u'_{\pm a}=(u_a-u_{-a})/2a, \quad . \quad . \quad . \quad . \quad . \qquad (6)$$

these being central divided differences of the data, and

$$u''_{\pm a}=u''_{\pm b}=\ .\ .\ .\ =0, \qquad u'''_{\pm a}=u'''_{\pm b}=\ .\ .\ .\ =0, \quad . \quad . \quad . \quad . \quad . \qquad (7)$$

We now give an example to show the systematic arrangement of the computation.

Example.—To find u_x, u_x', u_x'', u_x''' from the following table of values (Comrie, 1937, p. 934, Ex. 5), where $x=0{\cdot}736921$.

The decimal part of the quadratic multipliers is $x(1-x)/2$ or 0·0969342199.

x	u	x	u
−4	0·9013042519	1	0·3867873682
−3	0·7867773246	2	0·2982961527
−2	0·6797722790	3	0·2139106129
−1	0·5772156649	4	0·1333735852
0	0·4796611346	5	0·0564461185

(i) u_x.

$u_{(1)}$	$u_{(3)}$	$u_{(5)}$	$u_{(7)}$	
4112205057·9				0·0969342199
157286122·2	107835160·1			1·0969 . . .
247669635·9	28006·8	39083·4		3·0969 . . .
383799840·1	17253·2	88·6	78·0	6·0969 . . .
566346703·3	02871·3	95·5	78·0	10·0969 . . .

$u_x=0{\cdot}4107839078.$

(ii) u_x'. $x-\frac{1}{2}=0{\cdot}236921.$

$u'_{(1)}$	$\Delta u_{(1)}$	$u'_{(3)}$	$\Delta u_{(3)}$	$u'_{(5)}$	$\Delta u_{(5)}$	$u'_{(7)}$	
−0928737664·0							0·0969 . . .
29731707·3	45081064·3	−17960656·4					1·0969 . . .
31723332·2	135464578·0	943058·4	− 7153·3	−971155·7			3·0969 . . .
34719627·7	271594782·2	916603·3	−17906·9	69·6	5·2	−40·9	6·0969 . . .
38731259·3	454141645·4	881222·6	−32288·8	87·9	12·1	1·0	10·0969 . . .

$u_x'=-0{\cdot}0917971141.$

(iii) u_x''. $2(x-\frac{1}{2})=0{\cdot}473842$.

$\Delta u'_{(1)}$	$u''_{(3)}$	$\Delta u'_{(3)}$	$u''_{(5)}$	$\Delta u'_{(5)}$	$u''_{(7)}$	$\Delta u'_{(7)}$	
− 994043·3	0044610044·8						1·0969 . . .
−2985668·2	683281·0	17598·0	570469·8				3·0969 . . .
−5981963·7	793379·4	44053·1	417·1	−13·9	523·7		6·0969 . . .
−9993595·3	940626·0	79433·8	347·5	−32·2	3·5	−0·1	10·0969 . . .

$u_x''=0{\cdot}0044570524$.

(iv) u_x'''. $3(x-\frac{1}{3})=0{\cdot}710763$.

$u'''_{(3)}$	$\Delta u''_{(3)}$	$u'''_{(5)}$	$\Delta u''_{(5)}$	$u'''_{(7)}$	$\Delta u''_{(7)}$	$u'''_{(9)}$	
−2982129·9							1·0969 . . .
85668·2	73236·2	−27765·5					3·0969 . . .
90981·9	183334·6	694·5	− 52·7	−865·2			6·0969 . . .
98078·6	330581·2	600·9	−122·3	− 4·5	−0·2	−6·4	10·0969 . . .

$u_x'''=-0{\cdot}0002927866$.

To describe the routine, we shall give working details of selected entries in the above four schemes. In (i), first column,

$$4112205057{\cdot}9=0{\cdot}736921\times3867873682+0{\cdot}263079\times4796611346,$$
$$4157286122{\cdot}2=(1{\cdot}736921\times2982961527+1{\cdot}263079\times5772156649)/3,$$
$$4247669635{\cdot}9=(2{\cdot}736921\times2139106129+2{\cdot}263079\times6797722790)/5.$$

In (i), third column,

$$39083{\cdot}4=(3{\cdot}0969\ \ldots\times35160{\cdot}1-1{\cdot}0969\ \ldots\times28006{\cdot}8)/2,$$
$$39088{\cdot}6=(6{\cdot}0969\ \ldots\times35160{\cdot}1-1{\cdot}0969\ \ldots\times17253{\cdot}2)/5,$$

and so on. The 0·0969342199 remains on the levers throughout.

In (ii), first column, headed $u'_{(1)}$, are the central divided differences of the u's, according to (6) above. Thus,

$$-0928737664{\cdot}0=3867873682-4796611346,$$
$$-0929731707{\cdot}3=(2982961527-5772156649)/3,$$

and so on. Entries in all columns headed Δ are obtained from corresponding columns in previous schemes by subtracting the first entry in such a column in turn from all the other entries. For example,

$$45081064{\cdot}3=157286122{\cdot}2-112205057{\cdot}9,$$
$$135464578{\cdot}0=247669635{\cdot}9-112205057{\cdot}9.$$

In the column of (ii) headed $u'_{(3)}$,

$$17960656{\cdot}4=(1{\cdot}0969\ \ldots\times28737664-0{\cdot}0969\ \ldots\times29731707{\cdot}3)\\ -0{\cdot}236921\times45081064{\cdot}3,$$
$$17943058{\cdot}4=(3{\cdot}0969\ \ldots\times28737664-0{\cdot}0969\ \ldots\times31723332{\cdot}2\\ -0{\cdot}236921\times135464578{\cdot}0)/3,$$

and so on.

The column of (iii) headed $u''_{(3)}$ is obtained by multiplying all entries in the preceding column $\Delta u'_{(1)}$ by 0·473842, adding to entries in $\Delta u_{(1)}$ and dividing the results by 1, 3, 6, 10 respectively. This is in accordance with (4) and (7) above. In the column headed $u''_{(5)}$,

$$
\begin{aligned}
570469\cdot 8 &= (3\cdot 0969 \ldots \times 610044\cdot 8 - 1\cdot 0969 \ldots \times 683281\cdot 0 \\
&\qquad + 0\cdot 473842 \times 17598 - 7153\cdot 3)/2, \\
570417\cdot 1 &= (6\cdot 0969 \ldots \times 610044\cdot 8 - 1\cdot 0969 \ldots \times 793379\cdot 4 \\
&\qquad + 0\cdot 473842 \times 44053\cdot 1 - 17906\cdot 9)/5.
\end{aligned}
$$

Finally, in (iv), entries in the column $u'''_{(3)}$ are obtained by multiplying entries in the first column of (iii) by 3, and dividing the results respectively by 1, 3, 6, 10. This is in accordance with (5) and (7) above. In the column headed $u'''_{(5)}$,

$$
\begin{aligned}
-27765\cdot 5 &= -(3\cdot 0969 \ldots \times 82129\cdot 9 - 1\cdot 0969 \ldots \times 85668\cdot 2 \\
&\qquad - 0\cdot 710763 \times 73236\cdot 2 - 3 \times 17598)/2, \\
-27694\cdot 5 &= -(6\cdot 0969 \ldots \times 82129\cdot 9 - 1\cdot 0969 \ldots \times 90981\cdot 9 \\
&\qquad - 0\cdot 710763 \times 183334\cdot 6 - 3 \times 44053\cdot 1)/5,
\end{aligned}
$$

and so on.

These details of typical entries should sufficiently illustrate the routine, which is uniform and easily mastered. It will be found a good exercise to continue the scheme on the same model and evaluate u_x^{IV}, u_x^{V}. These will prove to be 0·0000217644 and −0·0000017322, though the last digits become uncertain as n and $n_{(2)}$ in (1) increase with higher derivatives.

We may check the derivatives so far found by forming the Taylor series

$$u_x + (1-x)u_x' + (1-x)^2 u_x''/2! + (1-x)^3 u_x'''/3! + \ldots,$$

where $1-x = 0\cdot 263079$. Taken to the fifth derivative, the series gives 0·38678736819, in good agreement with u_1, which is 0·3867873682. The check does not of course verify the correctness of the later digits of the higher derivatives, since these are associated in the Taylor series with numerically small coefficients.

It is to be observed that the method of this section is available only when u_x and derivatives of *consecutive* order are required at the same time. This limits its field of application to a certain extent, but the case does arise in statistical or practical mathematics where u_x and u_x' together, or even u_x, u_x', and u_x'' together are required.

3. INVERSE INTERPOLATION BY QUADRATIC CROSS-MEANS.

In direct interpolation as effected by quadratic cross-means the degree of the interpolating polynomial increases by two at each stage. The rapidity of convergence secured in this way is one of the chief advantages of the method; and it is natural to inquire whether quadratic cross-means cannot also be made available for *inverse* interpolation. Such an inquiry led to the method here proposed.

Suppose that we have as before the tabular values u_a, u_{-a}, u_b, u_{-b}, u_c, u_{-c}, . . . The problem now is, given u_x, to determine x. It is necessary for the success of the method that u shall be strictly monotonic over the tabular range used; and it is desirable also, though not absolutely necessary, that x shall lie within the central panel, and that the tabular intervals of x shall be not only equal, but as small as can be conveniently arranged.

The essence of the method consists in constructing from the tabular u's and u_x a certain function $v_h \equiv v(h, x)$, where $h=a, b, c, \ldots$, possessing properties suitable for quadratic extrapolation by cross-means. In particular, (i) v_h is an *even* function of h, (ii) $v_x = x$. The values v_h, like the linear cross-means $u_{\pm h}$ in the corresponding case of direct interpolation, are made the basis of further interpolation. They are subjected to extrapolation by quadratic cross-means, values v_ξ and $v_{\xi+\epsilon}$ being thus found, where ξ, ascertained by inspection and trial from the v_h themselves, is already a close approximation to x, and ϵ is small. In favourable cases linear interpolation between v_ξ and $v_{\xi+\epsilon}$ is possible, and will give x with a degree of accuracy which may be tested by the methods of § 4 of this paper.

The function v_h arises naturally when we consider *linear* interpolation for u_x between symmetrically placed pairs of values u_h and u_{-h}. If u_h were linear in h, x would be given accurately by the linear cross-mean

$$v_h = \{h(u_x - u_{-h}) - h(u_h - u_x)\}/(u_h - u_{-h}). \quad . \quad . \quad . \quad (1)$$

(Compare Whittaker and Robinson, p. 93, on the "rule of false position" for solving algebraic equations.)

This function v_h, which may also be written in the form

$$v_h = 2h(u_x - u_{-h})/(u_h - u_{-h}) - h, \quad . \quad . \quad . \quad . \quad (2)$$

is computed for $h=a, b, c, \ldots$ by means of either (1) or (2) and is made the subject of further interpolation. By inspection of (1) it is seen that $v_h = v_{-h}$, so that, provided v_h is representable with sufficient accuracy by a polynomial in h^2 of not too high degree, the method of quadratic cross-means is available. Also, by putting $h=x$ in (1), we have $v_x = x$.

The procedure is to interpolate for v_ξ, where ξ is an approximation to x. For a first tentative value of ξ we may take the first two or three digits of v_a, which is itself a linear approximation to x; for a second and better value of ξ the quadratic cross-mean of v_a and v_b based on the first value of ξ will usually serve. It would indeed be possible in many cases to evaluate v_ξ, to take this value as a new ξ and so evaluate a new v_ξ, to take this again as a new ξ and evaluate a new ξ, and so to iterate until convergence to a steady v_ξ was visible; this would be the value of x required. While this would often require no more than four iterations, we ourselves have found it more advantageous to obtain by two or three trials a ξ close to x (numerical criteria for accuracy are developed in § 4) and to evaluate v_ξ and $v_{\xi+\epsilon}$, where ϵ is 0·001, 0·0001, or some such convenient small number. The final step, if linear interpolation of v_h within the small interval $h=\xi$ to $h=\xi+\epsilon$ is judged permissible, is to evaluate x by

$$\xi+\epsilon(v_\xi-\xi)/(\epsilon-v_{\xi+\epsilon}+v_\xi). \quad . \quad . \quad . \quad . \quad (3)$$

Since the theory of the method is concerned with circumstantial details neither very interesting for their own sake nor capable of brief statement, while in practice the same details are ascertained by numerical examination of entries, we shall postpone further explanation and work out an example.

Example.—Given the tabular values of the example of § 2, to find (Comrie, 1937, p. 938, Ex. 5A) the value of x for which $u_x=0·4107839078$.

The values v_h are first computed. This can be done either according to (1) above, by subtracting u_x from each tabular u and taking the results as multipliers for linear cross-means of symmetrically placed pairs of values of x, namely, 0, 1; -1, 2; -2, 3, and so on; or, perhaps more easily, according to (2), by dividing u_x-u_0, u_x-u_{-1}, u_x-u_{-2}, . . . by the central divided differences u_1-u_0, $(u_2-u_{-1})/3$, $(u_3-u_{-2})/5$, . . . and subtracting 0, 1, 2, . . . from the results in turn. The values v_h so found are in the first column below.

A tentative cross-mean of the first two v's, with quadratic multipliers 0·0962, 1·0962 corresponding to $\xi=0·74$ (this value being suggested by the first v), gives at once 0·73696. A second trial with multipliers 0·09692, 1·09692 corresponding to $\xi=0·737$ gives 0·73692. Such trials take only a few seconds to perform, thus: set up 1·09692 as multiplicand on the setting levers, multiply by 741622 by addition turns, pull the 1 of 1·09692 to 0, multiply by 790105 by subtraction turns, and read off. We adopt $\xi=0·73692$, compute and record $\xi(1-\xi)/2=0·0969344568$, and proceed to interpolate for v_ξ.

$v^{(1}$	$v^{(2}$	$v^{(3}$	
741621982·9			0·0969344568
790105207·6	736922287·8		1·0969 . . .
886998338·5	24656·9	20988·4	3·0969 . . .
1032154729·9	28210·6	8·4	6·0969 . . .
1225354319·7	32949·8	8·3	10·0969 . . .

$\epsilon=0·00001$, $\quad \xi+\frac{1}{2}\epsilon-\frac{1}{2}=0·236925$.

$\epsilon\mathbf{\Delta}v^{(1}$	$\epsilon\Delta v^{(2}$			$v_{\xi+\epsilon}-v_{\xi}$
484·83			1·0969	
4·59	0·024	4·97	3·0969	484·97 × 0·236925
4·22	0·059	4·98	6·0969	
3·73	0·107	4·98	10·0969	= 114·9

ξ	v_{ξ}	$v_{\xi}-\xi$	
73692	736920988·4	9884	
3	21103·3	−88967	20999·9
		98851	

$x = 0·736921000.$

[*Note* 1.—The last step, simple linear interpolation between 73692 and 73693 with proportional parts 9884 and 88967, is most simply effected by finding 9884/98851 = 0·09999.

Note 2.—The various notations for divided differences have never seemed satisfactory to the author, being liable to confusion with other bracket-notations. For several years he has used in lectures a notation in which Newton's formula of divided differences appears as

$$u_x = u_a + (x-a)\mathbf{\Delta} u_{a,\,b} + (x-a)(x-b)\mathbf{\Delta}^2 u_{a,\,b,\,c} + \ldots,$$

the descriptive intention of the symbol $\mathbf{\Delta}$ being evident, and the suffixes denoting the arguments of the u's which enter into the respective differences. When the u's and their order are fixed, the simpler form

$$u_a + (x-a)\mathbf{\Delta} u_a + (x-a)(x-b)\mathbf{\Delta}^2 u_a + \ldots,$$

may be used, or the suffixes may even be omitted provided it is understood that u, $\mathbf{\Delta} u$, $\mathbf{\Delta}^2 u$, . . . denote the leading term and leading divided differences.]

In the computation for $v_{\xi+\epsilon}-v_{\xi}$, the entries in the column named $\epsilon\mathbf{\Delta}v^{(1}$ are divided differences of the v_h, considered as functions of $\frac{1}{2}h^2$, obtained by subtracting the first v_h from each of the others in turn and dividing the results by 1, 3, 6, 10. The next column, named $\epsilon\Delta v^{(2}$, contains the results of subtracting the first $v^{(2}$ from the others in turn; and the entries in the following column are obtained thus:

$$4·97 = (\ 3·097 \times 4·83 - 1·097 \times 4·59 + 0·024)/2,$$
$$4·98 = (\ 6·097 \times 4·83 - 1·097 \times 4·22 + 0·059)/5,$$
$$4·98 = (10·097 \times 4·83 - 1·097 \times 3·73 + 0·107)/9.$$

The procedure is exactly like that used in § 2 and based on § 2 (3) for computing u_x' from the scheme for u_x. In strict theory (as in § 4 below) the quadratic multipliers used in this computation of $v_{\xi+\epsilon}-v_{\xi}$ should be those for $\xi+\epsilon$ or 0·73693, not those for ξ or 0·73692, but when ϵ is small the digits required in $v_{\xi+\epsilon}-v_{\xi}$ are usually so few that this is an unnecessary refinement, the multipliers themselves being cut down to fewer digits. An alternative way of computing $v_{\xi+\epsilon}$, which would not take long, would be to compute it by cross-means in the same manner as v_ξ, with decimal part of quadratic multipliers $0{\cdot}73693 \times 0{\cdot}26307/2 = 0{\cdot}0969320876$. We ourselves have found the method of computing the increment $v_{\xi+\epsilon} - v_\xi$ more rapid, convergence being usually established at the very first set of cross-means.

4. General Criteria for Convergence and Accuracy.

The computer will wish to have definite information on the following points: (i) how to choose a good value of ξ for beginning the interpolation for v_ξ, and in so doing to judge beforehand the size of the interval ϵ; (ii) how to estimate the accuracy of the result given by the final linear interpolation between v_ξ and $v_{\xi+\epsilon}$. The error will consist of three components: (*a*) that due to stopping short the interpolation of v_ξ and $v_{\xi+\epsilon}$ at a certain order of cross-means; (*b*) that due to tabular error in rounding off the data u_h, and the derived values v_h, to so many places of decimals; (*c*) that due to the fact that the final interpolation between v_ξ and $v_{\xi+\epsilon}$ is linear.

(i) Differentiating v_h, as given in § 3 (1) or (2), and putting $h=x$ in the result, we obtain

$$[v_h']_{h=x} = 1 - 2xu_x'/(u_x - u_{-x}) \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \qquad (1)$$

$$= -x(u_0'' + \tfrac{1}{3}xu_0''' + \tfrac{1}{6}x^2u_0^{\text{IV}} + \ldots)/(u_0' + \tfrac{1}{6}x^2u_0'' + \ldots). \qquad (2)$$

Now in the immediate neighbourhood of $h=x$ the ratio of $v_h - v_x$, that is of $v_h - x$, to $h-x$, is nearly v_h'. Hence by (2) above, in order that this ratio may be small a first requisite is that x itself shall be small. This condition is one which is basic in all methods of inverse interpolation, and is fulfilled in practice by making the interval of tabulation of u as small as conveniently possible, and by arranging that x shall fall in the central interval and preferably near to the centre of it. If the series in the numerator and denominator of (2) converge in such a way that the first terms dominate, and for this it is necessary that values of u''' in the range x to $-x$ should be small compared with u_0' and u_0'', then the proportionate error committed by taking v_ξ instead of ξ for x will be nearly $-xu_0''/u_0'$. When the functional form of u is not given, or is not tractable when given, the computer may estimate the derivatives u_0' and u_0'' by central or mean central differences, evaluating for example

$$-x\mu\delta^2u_0/\delta u_0.$$

The expressions $-xu_0''/u_0'$ and $-x\mu\delta^2u_0/\delta u_0$ are not altered by changes of scale in x, such as the computer will usually make in order to work always with a unit interval and a central panel $-\frac{1}{2}$ to $\frac{1}{2}$, or 0 to 1.

Applying these considerations to the worked example of § 3, we have

$$\delta u_0 = 0\cdot3868 - 0\cdot4797 = -0\cdot093,$$
$$\mu\delta^2 u_0 = (0\cdot2983 - 0\cdot3868 - 0\cdot4797 + 0\cdot5772)/2 = 0\cdot0045,$$

while x, measured from the centre, is about 0·237, and would be preliminarily estimated as about $\frac{1}{4}$. We conclude that the error committed by taking v_ξ instead of ξ for x will be reduced to about $0\cdot25 \times 0\cdot0045/0\cdot093$, let us say 1/80 of what it was. It is true that in practice we shall take not v_ξ, but the approximation to v_ξ given by the cross-mean of the first two v's; at the same time this cross-mean, being correct as far as third differences, will usually be sufficiently close.

These conclusions are verified in the example. If we take $\xi = 0\cdot74$, quadratic multipliers 0·0962, 1·0962, we obtain a first cross-mean 0·736958. Since $x = 0\cdot736921$, the respective errors are 0·003079 and 0·000037, the second being evidently about 1/80 of the first. Again, if we take $\xi = 0\cdot737$, multipliers 0·0969155, 1·0969155, we obtain the cross-mean 0·7369232. The respective errors are 0·000079 and 0·0000022. It is true that the visible reduction of error is more nearly 1/40 than 1/80, but the reason is that the error has now become so small that remainder terms after the first cross-mean—that is, after third differences—have relative importance. Had we proceeded to more exact interpolation for v_ξ, where $\xi = 0\cdot737$, we should have obtained 0·7369219, the error being 0·0000009, again about 1/80 of the former error 0·000079.

In practice the reduction of error in v_ξ as compared with ξ will often be estimated from the difference of the first two v's. For we have

$$v_\xi = v_{\frac12} + \tfrac{1}{2}(\tfrac{1}{4} - \xi^2)\Delta v_{\frac12,\frac32} + R_\xi, \qquad . \quad . \quad . \quad . \quad (3)$$

$$v_{\xi+\epsilon} = v_{\frac12} + \tfrac{1}{2}\{\tfrac{1}{4} - (\xi+\epsilon)^2\}\Delta v_{\frac12,\frac32} + R_{\xi+\epsilon}, \qquad . \quad . \quad . \quad (4)$$

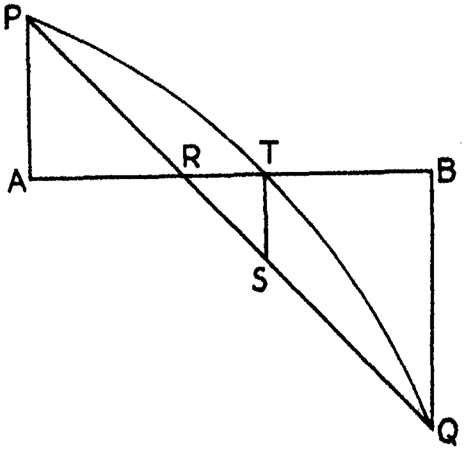
where $\Delta v_{\frac12,\frac32} = v_{\frac32} - v_{\frac12}$ and R_ξ, $R_{\xi+\epsilon}$ are remainder terms depending on fourth and higher differences or derivatives. By subtraction the proportionate change in v_ξ induced by a small change ϵ in ξ is nearly $\xi\Delta v_{\frac12,\frac32}$. Thus, taking again the example of § 3, we find

$$\xi\Delta v_{\frac12,\frac32} = 0\cdot237 \times 0\cdot0485 = 0\cdot0115, \quad \text{nearly } 1/87.$$

The conclusion is that it will be advantageous in practice so to choose the interval of tabulation that xu_0''/u_0', $x\mu\delta^2 u_0/\delta u_0$ or $x\Delta v_{\frac12,\frac32}$ is of the order of 1/50 or 1/100 or less. If this is done, two trials will usually give a sufficiently accurate ξ, thus ensuring that the interval ϵ will be small enough for the final linear interpolation.

(ii) Before examining this linear interpolation we shall consider the other two sources of error, due to cutting short the interpolation of v_ξ and $v_{\xi+\epsilon}$ at a certain stage, and to tabular error in the v_h. A paper by W. F. Sheppard (Sheppard, 1906) has been devoted to these matters, and we shall use his results. In the first place, we judge the accuracy of v_ξ and $v_{\xi+\epsilon}$ by the convergence to equality of cross-means in a column at some stage. (In the case of $v_{\xi+\epsilon}-v_\xi$ these are cross-means of divided differences.) Then, in regard to tabular error, quadratic extrapolation is equivalent in its results to interpolation by the Newton-Bessel formula to an odd order of differences, and for this it has been shown by Sheppard that the maximal tabular error for interpolation within a central panel up to the seventh differences, involving in our method the use of a quadratic multiplier with 10 for its integer part, is very slightly less than one and a half times the maximal tabular error of any datum. An examination of the data v_h in the example of § 3 will show that the tabular error in any of them does not exceed a quarter of a unit in the ninth decimal. It follows that the maximal tabular error in v_ξ and $v_{\xi+\epsilon}$, and of the value 0·736921000 for x, which is a weighted mean of v_ξ and $v_{\xi+\epsilon}$ with *positive* weights, is three-eighths of a unit in the ninth decimal. (It goes without saying that this maximal error, or even half of it, is in the highest degree improbable in practice.)

It remains to consider the linear interpolation between v_ξ and $v_{\xi+\epsilon}$. This is really linear *inverse* interpolation on the function v_h-h, the problem being to find for what value of h this function vanishes between the two values $v_\xi-\xi$ and $v_{\xi+\epsilon}-\xi-\epsilon$.



In the diagram here given, let $AB=\epsilon$, let AP and BQ be ordinates representing $v_\xi-\xi$ and $v_{\xi+\epsilon}-\xi-\epsilon$, let PTQ be the curve of the function v_h-h, and let $PRSQ$ be a straight line, where ST is perpendicular to AB. Then the error in x committed by linear interpolation is TR, while the error in v_x-x is TS; and the ratio $TR:TS$ is evidently $AB:AP+QB$, that is, $\epsilon:\epsilon-v_{\xi+\epsilon}+v_\xi$. Let the true value of x be $\xi+\theta\epsilon$, $0<\theta<1$. Then the error TS of linear interpolation in v_x-x is known to be $\frac{1}{2}\epsilon^2\theta(1-\theta)v''$, where v'' is taken at some point within the small range ϵ of interpolation. The error TR in x is found by multiplying this by $\epsilon/(\epsilon - v_{\xi+\epsilon} + v_\xi)$, but in all practical cases this factor differs but slightly from 1. Thus, in the example of § 3 it is 10000/9885·1, about 88/87. Again, the greatest value of $\theta(1-\theta)$ is $\frac{1}{4}$, attained when $\theta = \frac{1}{2}$, that is, in the centre of the interval. Differentiating (3) twice we see that v'' is nearly equal to $\Delta v_{\frac{1}{2}, \frac{3}{2}}$, the difference of the first two v's. Hence the possible error of linear interpolation may be estimated as $\frac{1}{8}\epsilon^2 \Delta v_{\frac{1}{2}, \frac{3}{2}}$, and will usually be less than this. In the example of § 3 this error is

$$(0{\cdot}00001)^2 \times 0{\cdot}0485/8, \quad \text{or} \quad 0{\cdot}00000\ 00000\ 006.$$

We conclude finally that the value 0·736921000 for x is free from error to the last place given. As a general precept we may lay it down that if x is desired correct to 10^{-2n}, it is well to have ϵ in the region of 10^{-n}, for then the error of linear interpolation will be negligible; it is worth while to make a third preliminary trial for ξ if so small an ϵ can be secured thereby.

Two minor points remain for explanation. The auxiliary computation for $v_{\xi+\epsilon} - v_\xi$ by cross-means of divided differences of the v's is based on the fact that the increment in a cross-mean such as

$$v_{\pm a, \pm b, \pm c} = \frac{\frac{1}{2}(c^2 - \xi^2) v_{\pm a, \pm b} - \frac{1}{2}(b^2 - \xi^2) v_{\pm a, \pm c}}{\frac{1}{2}(c^2 - b^2)}, \qquad (5)$$

produced by changing ξ to $\xi + \epsilon$ is

$$\epsilon(\xi + \tfrac{1}{2}\epsilon) \frac{v_{\pm a, \pm c} - v_{\pm a, \pm b}}{\frac{1}{2}(c^2 - b^2)}, \qquad (6)$$

as is readily verified. It follows that the increment $v_{\xi+\epsilon} - v_\xi$ can be computed by beginning with a first column of divided differences of the v_h and forming cross-means of these with the quadratic multipliers for $\xi + \epsilon$, but adding to the numerators of cross-means before division at each stage a difference of cross-means obtained at the corresponding stage in finding v_ξ. The result is multiplied by $\epsilon(\xi + \frac{1}{2}\epsilon)$, and it is well to introduce the factor ϵ at once into the scheme of cross-means, as we have done in the example of § 3, in order to see without delay how many digits are required in $v_{\xi+\epsilon} - v_\xi$ and at what stage convergence is established. The procedure is almost exactly that used in § 2 for finding u_α', which is indeed its limiting case $\epsilon = 0$. The only point of difference is that in the present application the multipliers are those for $\xi + \epsilon$, not for ξ, but since several digits are usually discarded because of the smallness of ϵ they can be discarded from the multipliers also, and the refinement becomes unnecessary.

The formula § 3 (3) of the final linear interpolation for x is justified as follows. We are to find x by linear interpolation between v_ξ and $v_{\xi+\epsilon}$, given that $v_x - x = 0$. It follows that

$$(x-\xi-\epsilon)(v_\xi-\xi)+(\xi-x)(v_{\xi+\epsilon}-\xi-\epsilon)=0,$$

whence

$$x-\xi=\epsilon(v_\xi-\xi)/(\epsilon-v_{\xi+\epsilon}+v_\xi).$$

As a concluding example, we shall find the value of z for which $\log_{10} z = 0·63827216$, given eight-place logarithms to base 10 of 1·5, 2·0, . . ., 6·5, 7·0. It is well known that widely spaced data in the beginning of the logarithmic table are not good material for polynomial interpolation, and the present method has in this case the same defect of slow convergence; we have therefore taken the interval of tabulation as $\frac{1}{2}$ instead of 1. An examination of tabular error shows that the seventh decimal of $v_{\frac{1}{2}}$ may be almost a unit in error; we shall, however, retain in the working both the seventh decimal and an additional digit as well, to stabilize the calculation.

The working is as follows. The entries u are the given tabular logarithms with 0·63827216 subtracted from each.

z	x	$-u$	z	x	u
1·5	−5	46218090	7·0	6	20682588
2·0	−4	33724216	6·5	5	17464120
2·5	−3	24033215	6·0	4	13987909
3·0	−2	16115091	5·5	3	10209053
3·5	−1	9420412	5·0	2	6069784
4·0	0	3621217	4·5	1	1494035

The v's are formed. Two trial cross-means give ξ almost steady at 0·6956. Then $\xi(1-\xi)/2 = 0·10587032$.

$v^{(1}$	$v^{(3}$	$v^{(5}$	$v^{(7}$	$v^{(9}$	$v^{(11}$	
7079254·4						0·10587032
8244595·5	6955879·4					1·105 . . .
10608955·4	54690·9	56536·6				3·105 . . .
14247115·1	52777·1	565·5	506·7			6·105 . . .
19294356·4	49932·7	610·1	504·0	510·8		10·105 . . .
25993099·8	45760·1	678·7	499·8	11·4	09·6	15·105 . . .

$v_\xi = 6956509·6$, $\epsilon = 0·0001$, $\xi+\frac{1}{2}\epsilon-\frac{1}{2} = 0·19565$.

$\epsilon\Delta v^{(1}$	$\epsilon\Delta v^{(3}$			$v_{\xi+\epsilon}-v_\xi$
116·53			1·10587	115·8 × 0·19565
117·66	−0·12	115·8	3·10587	
119·46	−0·31	115·8	6·10587	= 22·7

ξ	v_ξ	$v_\xi - \xi$	
6956	69565096	5096	
6957	5323	−4677	5214
		9773	

Since only six decimals can be trusted, $x=0{\cdot}695652$, $z=4{\cdot}347826$.

In conclusion let us insist again that the important point in the method proposed in this paper is to secure a good value of ξ, and therefore a small value of ϵ. It is possible that in difficult cases a sufficiently small ϵ cannot be obtained at the first stage, so that the final linear interpolation is not exact enough. In such a case we would use the value given by this first inverse interpolation as a suitable ξ with which to carry out a second; but the case is unlikely. Such difficulties seldom arise if (i) u is tabulated at a sufficiently fine interval, (ii) x is near the centre of the centre panel, (iii) ϵ is sufficiently small. If u_x is very close to one of the tabular u's, it is often advantageous to omit that u from the working and to take the central panel as u_{-1} to u_1, with quadratic multipliers as in § 1, no longer halved. For many practical purposes, when x is required to a few digits only, the method will give x correctly with no more than the first few trial cross-means.

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[Added June 1, 1938. The new notation Δ for divided differencing having aroused some interest, the author ventures on a modification, by which Newton's formula appears thus:

$$u_x = u_a + (x-a)\underset{b}{\Delta} u_a + (x-a)(x-b)\underset{bc}{\Delta}^2 u_a + \ . \ . \ .$$

The symbol of operation is here detached from, and prefixed to, the operand u_a, the arguments implied in the operation being indicated by the suffixes. Admittedly this notation does not bring out the symmetrical nature of divided differences; on the other hand, it does bring out their operational analogy with ordinary differencing and differentiation.]

(*Issued separately July* 7, 1938.)

XII.—Green's Function for an Ellipse, and its Application to the Motion of a Point Vortex. By **D. Meksyn,** D.Sc.

Communicated by Professor E. T. WHITTAKER, F.R.S.

(MS. received February 28, 1938. Revised MS. received May 18, 1938.
Read May 2, 1938.)

1. GREEN'S FUNCTION FOR A PLANE EXTERNAL TO AN ELLIPSE.

GREEN'S function for a plane external to an ellipse, expressed as an infinite sum, was derived in a previous paper (Meksyn, 1937). For the sake of convenience this derivation is sketched here.

We introduce elliptic co-ordinates

$$x = c \cosh \xi \cos \eta, \qquad y = c \sinh \xi \sin \eta. \quad . \quad . \quad . \quad (1.1)$$

The equation to the ellipse is

$$\frac{x^2}{c^2 \cosh^2 \xi_0} + \frac{y^2}{c^2 \sinh^2 \xi_0} = 1, \quad . \quad . \quad . \quad . \quad (1.2)$$

and Poisson's equation becomes

$$\left.\begin{aligned} \frac{\partial^2 \psi}{\partial x^2} + \frac{\partial^2 \psi}{\partial y^2} = h^2\left(\frac{\partial^2 \psi}{\partial \xi^2} + \frac{\partial^2 \psi}{\partial \eta^2}\right) = \zeta, \\ \text{where} \qquad \frac{1}{h^2} = c^2(\cosh^2 \xi - \cos^2 \eta). \end{aligned}\right\} \quad . \quad . \quad . \quad (1.3)$$

The region in the plane (ξ, η) corresponding to the plane (x, y) external to the ellipse (1.2) is a strip bounded by lines

$$\eta = 0, \qquad \eta = 2\pi, \qquad \xi = \xi_0. \quad . \quad . \quad . \quad . \quad (1.4)$$

The solution of (1.3) is based on Green's formula,

$$\iint (u\nabla^2 v - v\nabla^2 u)\,dxdy = \int\left(u\frac{dv}{\partial n} - v\frac{\partial u}{\partial n}\right)ds, \quad . \quad . \quad . \quad (1.5)$$

where the differentiation $\frac{\partial}{\partial n}$ is taken along the external normal.

Inserting in (1.5) instead of u Green's function corresponding to the region of integration one obtains, in the well-known way, the expression for v, if the latter satisfies Poisson's equation.

One of the conditions which Green's function is required to satisfy is that the integral

$$\int u\frac{\partial v}{\partial n}ds \; . \qquad . \qquad . \qquad . \qquad . \qquad . \qquad . \quad (1.6)$$

taken round the boundary shall vanish; this is usually achieved by making u vanish on the boundary.

Such a procedure, however, cannot be applied in our case, since it would make $\eta=0$ and $\eta=2\pi$ or $y=0$ a stream line, which would correspond to a case when there is an infinitely thin, infinitely long screen along the axis of x.

We can, however, make the integral (1.6) vanish if u vanishes along $\xi=\xi_0$, and if u and v are periodic functions in η with a period 2π. The integrand (1.6) along the line $\xi=\xi_0$ from $\eta=0$ to $\eta=2\pi$ will vanish, and the integrands along the lines $\eta=0$ and $\eta=2\pi$ will mutually cancel out; for, when the integrand is periodic in η with period 2π, $\dfrac{\partial v}{\partial n}$ has opposite signs at the corresponding points, since the normal is always an external one.

Now, Green's function for an infinite half-plane, bounded at one side by the line $\xi=\xi_0$, is

$$\frac{1}{4\pi}\log\frac{(\xi-\xi')^2+(\eta-\eta')^2}{(\xi+\xi'-2\xi_0)^2+(\eta-\eta')^2}. \qquad . \qquad . \qquad . \quad (1.7)$$

It vanishes along the line $\xi=\xi_0$.

The function sought, however, must be periodic in η with period 2π; so that the expression for Green's function will be

$$G(\xi',\eta';\ \xi,\eta)=\frac{1}{4\pi}\sum_{n=-\infty}^{n=\infty}\log\frac{(\xi-\xi')^2+(\eta-\eta'-2\pi n)^2}{(\xi+\xi'-2\xi_0)^2+(\eta-\eta'-2\pi n)^2}. \quad . \quad (1.8)$$

The solution of (1.3) is then

$$\psi(\xi,\eta)=\int_{\xi'=\xi_0}^{\infty}\int_{\eta'=0}^{2\pi}\zeta(\xi',\eta')G(\xi',\eta';\ \xi,\eta)\frac{\partial\xi' d\eta'}{h^2},$$

$$\frac{1}{h^2}=c^2(\cosh^2\xi'-\cos^2\eta'). \qquad . \qquad . \qquad . \qquad . \quad (1.9)$$

The sum (1.8) can be expressed in circular and hyperbolic functions by making use of the relation

$$\sin z=z\prod_{n=1}^{\infty}\left(1-\frac{z^2}{\pi^2 n^2}\right), \qquad . \qquad . \qquad . \qquad . \quad (1.10)$$

and after some reductions we get

$$G(\xi',\eta';\ \xi,\eta)=\frac{1}{4\pi}\log\frac{\cosh(\xi-\xi')-\cos(\eta-\eta')}{\cosh(\xi+\xi'-2\xi_0)-\cos(\eta-\eta')}. \quad . \quad (1.11)$$

2. MOTION OF A POINT VORTEX OUTSIDE AN ELLIPSE.

Consider a point vortex of strength k situated at x', y' outside an ellipse $\xi = \xi_0$.

The corresponding stream function is

$$\psi = \frac{k}{2\pi} \log \frac{\cosh(\xi - \xi') - \cos(\eta - \eta')}{\cosh(\xi + \xi' - 2\xi_0) - \cos(\eta - \eta')} . \qquad (2.1)$$

By a well-known procedure (Ramsey, 1935, p. 224) the stream function χ corresponding to the motion of the vortex itself is found to be

$$\chi = -\frac{k}{4\pi} \log \sinh(\xi' - \xi_0) - \frac{k}{8\pi} \log(\cosh^2 \xi' - \cos^2 \eta') . \qquad (2.2)$$

The function χ can be expressed in a very simple form in the plane (x, y).

Let r and r_1 be the corresponding distances of the point x', y' from the foci $(c, 0)$ and $(-c, 0)$.

It can be easily shown that

$$\chi = -\frac{k}{8\pi} \log \{[a\sqrt{(r + r_1 - 2c)(r + r_1 + 2c)} - b(r + r_1)^2] r r_1\}, \qquad (2.3)$$

where $2a$ and $2b$ are the major and minor axes; the ellipse itself is a stream line $\chi = \infty$; the term in brackets vanishes in that case.

The motion of a vortex outside of a line of length $2c$ is found from (2.3) by putting $b = 0$; the latter case was also considered by Barth (1930).

The complex potential function corresponding to the vortex outside an ellipse is

$$\phi + i\psi = \frac{ik}{2\pi} \log \frac{\sinh \dfrac{\xi + i\eta - (\xi' + i\eta')}{2}}{\sinh\left(\dfrac{\xi + i\eta + \xi' - i\eta'}{2} - \xi_0\right)} . \qquad (2.4)$$

3. GREEN'S FUNCTION FOR AN AREA BOUNDED BY TWO CONFOCAL ELLIPSES.

Consider the plane enclosed between two confocal ellipses $\xi = \xi_1$ and $\xi = \xi_2$ $(\xi_2 > \xi_1)$.

The corresponding region in the plane ξ, η is a rectangle bounded by lines

$$\xi = \xi_1, \quad \xi = \xi_2; \qquad \eta = 0, \quad \eta = 2\pi . \qquad (3.1)$$

Consider a point ξ', η' inside this rectangle. The images at this point in the lines $\xi = \xi_1$ and $\xi = \xi_2$ are:

$2\xi_1 - \xi'$ reflected in $\xi = \xi_1$	$2\xi_2 - \xi'$ reflected in $\xi = \xi_2$
$2\xi_2 - 2\xi_1 + \xi'$,, ,, ξ_2	$2\xi_1 - 2\xi_2 + \xi'$,, ,, ξ_1
$4\xi_1 - 2\xi_2 - \xi'$,, ,, ξ_1	$4\xi_2 - 2\xi_1 - \xi'$,, ,, ξ_2
. . .	. . .

The co-ordinate η' remains, of course, unchanged.

It can be shown that the two series of images, including the point ξ', η' itself, may be expressed as

$$\left.\begin{array}{c} \xi' \pm 2m(\xi_2-\xi_1) \\ 2\xi_1-\xi' \pm 2m(\xi_2-\xi_1) \\ m=0,\ 1,\ 2\ \ldots \end{array}\right\}, \qquad (3.2)$$

where the former correspond to sources and the latter to sinks.

Green's function is also periodic in η' with a period 2π; whence

$$G(\xi', \eta';\ \xi, \eta)=\frac{1}{4\pi}\sum_{m=-\infty}^{\infty}\sum_{n=-\infty}^{\infty}\log\frac{[\xi-\xi'-2m(\xi_2-\xi_1)]^2+(\eta-\eta'-2\pi n)^2}{[\xi+\xi'-2\xi_1-2m(\xi_2-\xi_1)]^2+(\eta-\eta'-2\pi n)^2}. \quad (3.3)$$

This sum is divergent; it can be transformed into a convergent expression. The order of summation is, however, very important.

Summing (3.3) first with respect to m, we get

$$G(\xi', \eta';\ \xi, \eta)=\frac{1}{4\pi}\sum_{n=-\infty}^{\infty}\log\frac{\sin\frac{\pi}{2\Omega}[a-i(b-2\pi n)]\sin\frac{\pi}{2\Omega}[a+i(b-2\pi n)]}{\sin\frac{\pi}{2\Omega}[c-i(b-2\pi n)]\sin\frac{\pi}{2\Omega}[c+i(b-2\pi n)]}, \quad (3.4)$$

where

$$\xi-\xi'=a, \qquad \eta-\eta'=b, \qquad \xi+\xi'-2\xi_1=c, \qquad \Omega=\xi_2-\xi_1>0. \quad (3.5)$$

Expressing the trigonometric functions by means of exponentials (3.4) can be summed with respect to n; and we finally get, after some reductions,

$$G(\xi, \eta;\ \xi', \eta')=\frac{1}{4\pi}\log\frac{\vartheta_1(\nu)\vartheta_1(\bar{\nu})}{\vartheta_1(\nu_1)\vartheta_1(\bar{\nu}_1)}, \quad (3.6)$$

where (Whittaker and Watson, 1927, p. 470)

$$\vartheta_1(\nu)=2q_0q^{\frac{1}{4}}\sin\nu\prod_{n=1}^{\infty}(1-q^{2n}e^{2i\nu})(1-q^{2n}e^{-2i\nu}), \qquad q_0=\prod_{n=1}^{\infty}(1-q^{2n});$$
$$\nu=\frac{[\xi-\xi'-i(\eta-\eta')]\pi}{2\Omega}; \qquad \nu_1=\frac{[\xi+\xi'-2\xi_1-i(\eta-\eta')]\pi}{2\Omega}; \quad (3.7)$$
$$\tau=\frac{i\pi}{\Omega}, \qquad q=e^{\pi i\tau},$$

and $\bar{\nu}$ and $\bar{\nu}_1$ are the conjugates at ν and ν_1.

It can be shown that G is constant on the boundary.

In fact, the ϑ_1 functions satisfy the relations,

$$\vartheta_1(\nu+m\pi+n\pi\tau)=(-1)^{m+n}q^{-n^2}e^{-2in\nu}\vartheta_1(\nu), \qquad \vartheta_1(-\nu)=-\vartheta_1(\nu), \quad (3.8)$$

where m and n are integers.

Since

$$\nu_1=-\bar{\nu} \quad \text{when} \quad \xi=\xi_1; \qquad \nu_1=-\bar{\nu}+\pi \quad \text{when} \quad \xi=\xi_2, \quad (3.9)$$

the ratio of the ϑ_1 functions is equal to unity in both cases.

The expression (3.6) is also periodic in η with a period 2π; since if

η is increased by $2\pi n$, ν and ν_1 are increased by $-\pi n\tau$; and it is easily found that the nominator and the denominator in (3.6) are multiplied by the same factor, the ratio remaining constant.

SUMMARY.

Green's function for a plane outside an ellipse and for a plane between two confocal ellipses are evaluated.

The motion at a point vortex outside an ellipse is found.

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XIII.—The Brackish-water Lochs of Orkney. By **Edith A. T. Nicol,** B.A., Ph.D., The Department of Natural History, The University of St Andrews. *Communicated by* THE PRESIDENT. (With Two Figures.)

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INTRODUCTION.

THE Lochs of Stenness and Harray are the only brackish-water lochs in Orkney. They are famous for their trout fishing, and they are the only known Scottish stations for *Neritina fluviatilis* L. Although Murray and Pullar (1910) pointed out that the fauna of Stenness was marine in character while the ordinary fresh-water plankton animals occurred in Harray, little else is known about the general fauna or about the conditions under which the animals are living. I visited the Mainland of Orkney in July 1936 to examine these lochs from an ecological point of view and to compare them with the brackish-water lochs of the Hebrides.

I wish to record my thanks to Miss M. D. Dunn of St Andrews University, who kindly identified the algæ for me, a complete list being published elsewhere (Dunn, 1937); and to Mr R. Elmhirst of Millport, Mr A. G. Lowndes of Marlborough College, Mr C. Oldham of Berkhamstead, Mr A. R. Waterston of the Royal Scottish Museum, and the Entomological Department of the Natural History Museum, South Kensington, for help in identifying the animals.

The collecting and chemical methods employed were the same as those used by me in North Uist, but boats being available in Orkney, water samples were obtained from deep water and a dredge and plankton net used. Oxygen was estimated by Winkler's method and calcium by shaking with soap solution, giving fairly accurate results for comparative purposes.

THE LOCH OF STENNESS.

The Loch of Stenness is about 2½ sq. miles in area, communicating with the sea to the east of Stromness by a narrow channel about half a mile long, known as the Bush, which passes under the road at Bridge of Waithe. The loch runs north-west for nearly 4 miles, and some 2 miles from Bridge of Waithe on the north-east side it receives the overflow from the Loch of Harray at Bridge of Brogar.

Both lochs were surveyed by Murray and Pullar (1910). The Loch of Stenness is flat-bottomed with an average depth of 10½ ft. The shores are flat, in many places with only a few inches of water for a distance of 50 yd. from the edge, and then shelve steeply. They consist, for the most part, of fragments of Stromness flagstones covered with a dense growth of weed, except at the heads of shallow bays where the bottom is sandy or muddy. The bottom of the loch is composed of fine black mud, covered in many places with a dense felt of non-rooting filamentous algæ.

The loch lies only 3 or 4 ft. above sea-level but it is little affected by the tides. The shallow and narrow outlet at Bridge of Waithe allows only a small amount of water to enter or leave the loch each day and it is only at spring tides that the level is appreciably raised. The following are the figures for the salinity, hydrogen ion concentration, calcium content, alkali reserve, and temperatures of the shore water at various points (fig. 1) round the Loch of Stenness on 17th July, 11 days after the new moon tides:—

Station.	Salinity ‰.	pH.	Alkali Reserve.	Calcium, mg. per litre	Temperature, ° C.
I.	16·6	9·4	0·0030 N.	56·0	19
II.	14·6	9·6	0·0026 N.	67·0	24
III.	15·8	..	0·0025 N.	..	..
IV.	11·2	9·8	0·0026 N.	56·0	22
V.	14·8	9·8	0·0025 N.	..	22
VI.	15·2	9·6	0·0025 N.	..	20
VII.	17·0	9·4	0·0026 N.	..	19
VIII.	15·8	9·6	0·0023 N.	..	19
IX.	15·4	9·4	0·0023 N.	89·0	22
X.	9·0	9·2	0·0025 N.	..	17
XI.	15·4	9·6	0·0026 N.	..	17
XII.	15·4	9·6	0·0024 N.	..	20
XIII.	15·4	9·6	0·0024 N.	56·0	18

In deeper water there is a well-marked difference in the salinity at the surface and at the bottom during July and probably throughout the year.

Date.	Bridge of Waithe, B. S. ‰.		Bridge of Brogar, A. S. ‰.	
	Bottom.	Surface.	Bottom.	Surface.
21st	26·8	18·4	23·0	17·0
28th	26·8	17·2	17·6	10·2

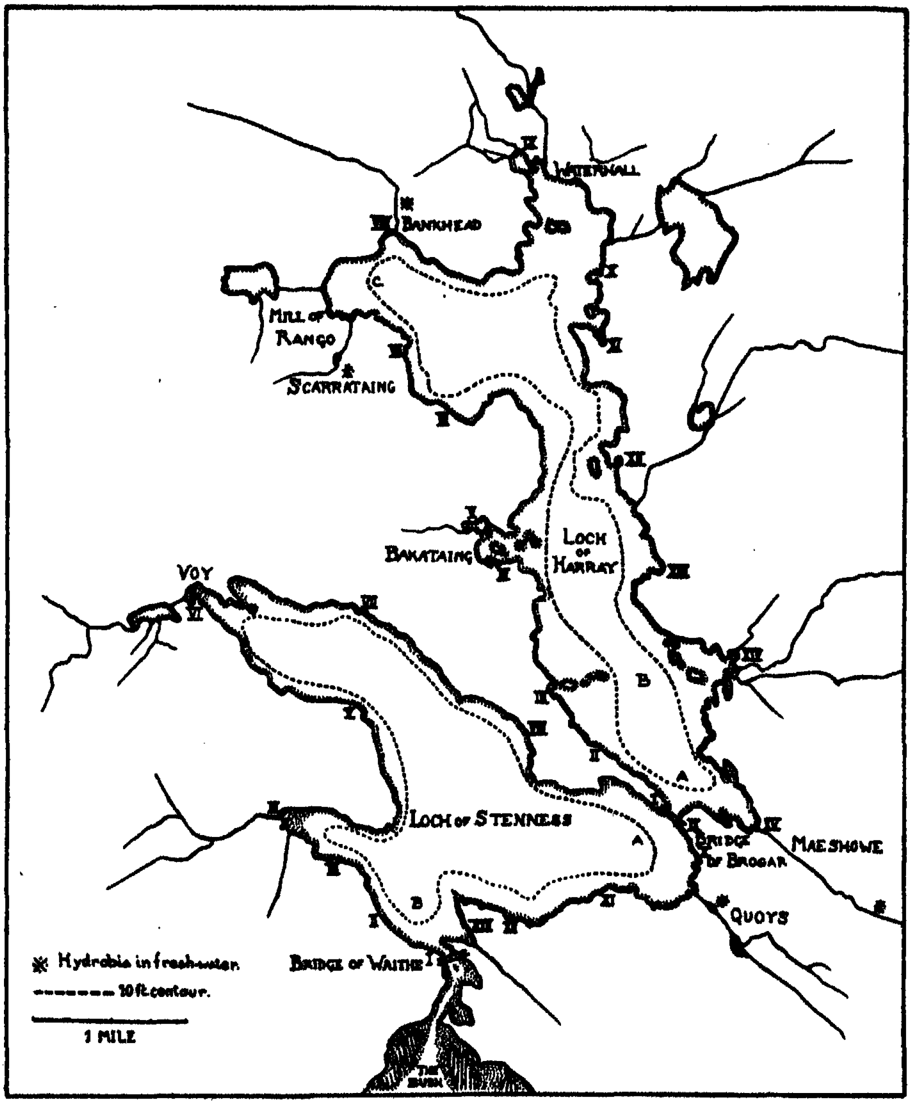

FIG. 1.—Map of the Lochs of Stenness and Harray to show the position of the collecting stations, and the occurrence of Hydrobia in streams.

Oxygen determinations were made at the surface and bottom at the same stations; even over black mud at the bottom there appears to be a plentiful supply of oxygen, at least during the summer months.

Date.	Temp., ° C.		Bridge of Waithe, B.				Bridge of Brogar, A.			
			Bottom.		Surface.		Bottom.		Surface.	
	Bottom.	Surface.	c.c. O_2.	% Sat.	c.c. O_2.	% Sat.	c.c. O_2.	% Sat.	c.c. O_2.	% Sat.
25th	16	19	..	..	..	..	5·44	88	7·11	117
27th	16	14·5	7·85	126	7·81	122	..	..	..	..

The vegetation of the loch is predominantly brackish in character, although a few marine algæ also occur, mostly near the outflow. The following are the principal species present round the shores: *Ruppia maritima* Linn., *Cladophora rupestris* Kütz., *C. flavescens* Harv., *C. fracta* Kütz., *Chætomorpha linum* Kütz., *Enteromorpha intestinalis* Link., *Ascophyllum nodosum* Le Jol, *Fucus vesiculosus* Linn., *F. ceranoides* Linn., *F. serratus* Linn., *Furcellaria fastigiata* Lamour, *Polysiphonia urceolata* Grev. *Potamogeton pectinatus* Linn. and the fresh-water alga *Zygnema anomalum* Hass. occur in one or two of the fresher bays.

The following occur in the deep water on the bottom mud: Bridge of Waithe, *Cladophora fracta*, *Chætomorpha litorea* Cooke, *Enteromorpha clathrata* Agard.; Bridge of Brogar, *Chætomorpha linum*, *Furcellaria fastigiata*, *Sphacelaria cirrhosa* Agard.

The following animals are to be found almost everywhere in shallow water where the bottom is suitable:—

Clava multicornis (Forsk.).

Procerodes ulvæ (Oersted).

Nereis diversicolor (O. F. Müller).

Jæra marina (Fab.).
Gammarus duebeni Lilljeborg.
Corophium volutator (Pallas).
Praunus flexuosus (Müller).
Neomysis vulgaris (J. V. Thompson).

Mya arenaria L.
Neritina fluviatilis (L.).
Hydrobia jenkinsi Smith.

Chironomus longistylus (Goet.).
Chironomus aprilinus (Mieg.).
Cricotopus vitripennis (Mieg.).

Anguilla vulgaris Turton.
Gasterosteus aculeatus (L.).
Gobius microps Kröyer.

Throughout a small area near Bridge of Waithe *Hydrobia jenkinsi* and *Neritina fluviatilis* are absent, but *Gonothyræa lovéni* (Allmann), *Littorina saxatilis* var. *rudis* (Maton), *Spinachia vulgaris* Flem. and *Gammarus campylops* Leach all occur here. A single specimen of *Gammarus zaddachi* Sexton was found among the *Gammarus duebeni* collected at Station XIII.

On the loch-bottom among weed and in the mud the following occur:—

Gammarus duebeni.	*Peringia ulvæ* Pennant.
Corophium volutator.	*Mya arenaria.*

Plankton samples were taken at stations A and B on several occasions and the following species recorded:—

Acartia clausi (Giesb.).
Cyclops strenuus (Fisch.).
Podon polyphemoides (Leuk.).
Evadne nordmanni (Lovén).

In addition *Cyclops viridis* (Jurine) and *Ectinosoma curticorne* Bœck. occur at Bridge of Waithe; and *Eurytemora velox* (Lilljeborg), *Daphnia longispina* O. F. Müller and *Alona affinis* Leydig at Bridge of Brogar, along with many veliger larvæ. These could not belong to any of the Gastropods living in the loch, but appeared to be the larvæ of *Littorina littorea* (L.).

Cod, herring, mullet, sillock, flounders, and other sea-fish are said to occur at times in the Loch of Stenness, and brown- and sea-trout are always present.

BRIDGE OF BROGAR.

The Lochs of Stenness and Harray must have been confluent at one time, the only barrier between them being a sill of rock some 50 yd. broad over which the water lay to the depth of 1 to 2 ft. A road now runs across the sill on a stone causeway pierced by a number of square conduits through which the two lochs communicate. The salinity in this shallow water is more variable than in either of the lochs. Usually water flows from Harray into Stenness, except at the March and September spring tides when the current flows in the opposite direction. Under exceptional circumstances other spring tides may reach the Loch of Harray, as happened in July 1936 when the spring tides filled the Loch of Stenness after a period of drought. Salt water was streaming from Stenness into Harray from the 16th to the 23rd, when the current was reversed owing to the level of Stenness beginning to fall after the spring tides. Fig. 2 shows the changes in salinity on each side of the road between the 16th and 30th July. The minor fluctuations are probably due to changes in the strength and direction of the wind.

The following plants occur in the shallow area at Bridge of Brogar, and are subjected to these sudden changes of salinity: *Ruppia maritima*, *Myriophyllum alterniflorum* DC., *Littorella lacustris* L. (Loch of Harray only) *Fucus ceranoides*, *Enteromorpha intestinalis*, *Chætomorpha linum*, and *Cladophora flavescens*.

The following animals also live in the same changeable environment:—

Procerodes ulvæ.	*Hydrobia jenkinsi.*
	Neritina fluviatilis.
Gammarus duebeni.	
Jæra marina.	*Gasterosteus aculeatus.*
Neomysis vulgaris.	*Anguilla vulgaris.*

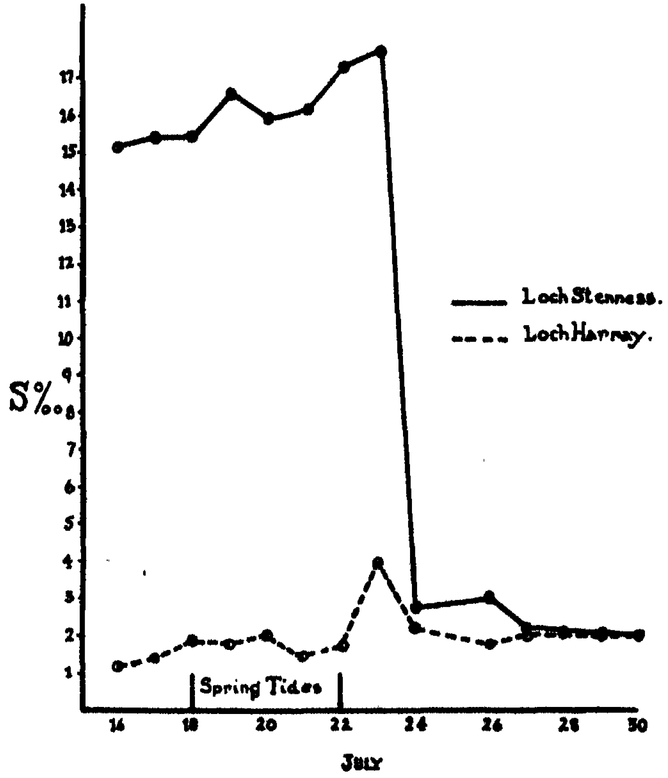

FIG. 2.—To show the changes in salinity of the two lochs in the shallow water at Bridge of Brogar from 16th to 30th July 1936.

THE LOCH OF HARRAY.

The Loch of Harray is about 4½ miles long with an area of 3¾ sq. miles. It is flat-bottomed with an average depth of 9 ft. and a maximum depth of 14 ft. The following are the figures for the salinity, hydrogen ion concentration, alkali reserve, calcium content, and temperature at various points (fig. 1) on 24th July:—

Station.	Salinity °/oo.	pH.	Alkali Reserve.	Calcium, mg. per litre.	Temperature, ° C.
I.	2·8	9·2	0·0024 N.	78	15
II.	1·2	9·0	0·0020 N.	..	16
III.	1·6	9·2	0·0021 N.	78	15
IV.	0·6	9·4	0·0020 N.	..	17
V.	0·6	9·8	0·0022 N.	..	17
VI.	1·0	9·4	0·0022 N.	..	17
VII.	0·9	9·4	0·0020 N.	..	17
VIII.	0·8	9·4	0·0020 N.	78	16
IX.	1·0	9·4	0·0024 N.	..	15
X.	1·4	9·6	0·0020 N.	..	16
XI.	1·2	9·5	0·0026 N.	78	15
XII.	1·4	9·6	0·0021 N.	..	15
XIII.	1·2	9·4	0·0033 N.	..	16
XIV.	1·2	9·4	0·0025 N.	78	16

In the southern part, where the water is deeper, there is a marked difference between the bottom and surface salinity, but this is almost obliterated in the shallower and more isolated northern portion.

Station.	Salinity °/oo.		Depth.
	Bottom.	Surface.	
I.	1·7	1·7	7 ft.
II.	4·3	1·7	13 „
III.	0·9	0·8	9 „

There is also a marked difference in the calcium content of the bottom and surface water at Station III, the figures being 139 and 78 mg. per litre respectively. The following are the figures for the oxygen content of the bottom and surface waters:—

Date.	Station.	Depth.	Oxygen. Bottom.		Oxygen. Surface.		Temp., ° C.	
			c.c. O_2.	% Sat.	c.c. O_2.	% Sat.	Bottom.	Surface.
22nd	I.	7 ft.	8·2	112	7·6	103	15	14
22nd	II.	13 „	8·7	121	7·3	100	15	14
27th	III.	9 „	8·1	110	9·1	126	16	15

The following are the most widely distributed species of plants found in the loch: *Myriophyllum alterniflorum*, *Littorella lacustris*, and *Cladophora flavescens*.

At the head of the loch, at Mill of Rango, Waterhall, and in general wherever the salinity is below 1 part per thousand, the following typically fresh-water species occur: *Menyanthes trifoliata* L., *Polygonum amphibium* L., *Potamogeton lucens* L., *P. heterophyllus* Schreb., *P. prælongus* Wulf., *P. filiformis* Pers., *Phragmites communis* Tnn., *Juncus balthicus* Willd., *Chara aspera* Willd., *C. baltica* Brügel, *Equisetum palustre* L., *Fontinalis antipyretica* L., *Cladophora holsatica* Kütz.

The following animals occur universally round the shores:

Spongilla lacustris (L.).

Glossosiphonia complanata (L.).
Jæra marina.
Gammarus duebeni.

Neritina fluviatilis.
Hydrobia jenkinsi.

Gasterosteus aculeatus.
Anguilla vulgaris.

Small shield-shaped caddis cases, probably belonging to a species of Hydroptila, were abundant everywhere under stones, but no adults were obtained.

The following fresh-water species occur in the fresher parts and particularly at Baikataing, Mill of Rango, and Waterhall:—

Hydra grisea L.

Glossosiphonia heteroclita (L.).
Helobdella stagnalis (L.).
Hæmopis sanguisuga (L.).

Plumatella repens (L.).

Cloëon sp.
Sialis lutaria L.

Ephemerella ignita Poda.
Leptocerus cinereus Curt.
Mystacides longicornis L.
Polycentropus flavomaculatus Pict.
Sigara distincta Fieb.

Limnæa peregra (Müller).
Planorbis contortus (L.).
Sphærium corneum (L.).

Plankton hauls were made at Stations A, B, and C. *Daphnia longispina* O. F. Müller, *Diaptomus laticeps* Sars, and *Cyclops strenuus* Fischer occur at all three stations, *Cyclops viridis* (Jurine) and *C. agilis* Koch at Station A, *C. agilis* at Station B, and *C. albidus* Jurine at Station C. The blue-green alga *Anabæna variabilis* Kütz. was present throughout the loch in the surface waters.

NOTES ON THE FAUNA.

Hydrobia jenkinsi.—Hydrobia occurs everywhere in the Lochs of Harray and Stenness except in a small area near Bridge of Waithe. In the Loch of Harray it is limited in distribution by its need of a solid substratum; at Mill of Rango, where the bottom is thickly covered with *Cladophora holsatica*, *H. jenkinsi* is present in small numbers, but near Bridge of Brogar in the same depth of water, where the bottom is muddy, it is absent. In the Loch of Stenness another limiting factor comes into play. Although large areas of the bottom are covered with weed giving as firm a substratum as at Mill of Rango, not a single specimen of *H. jenkinsi* was obtained from deep water. This appears to be due to the higher salinity of the bottom water. The salinity limits of the species in

North Uist are 0 to 23 parts per thousand (Nicol, 1936) and in Randersfjord in Jutland 1 to 20 parts per thousand (Johanssen, 1918).

Elsewhere on the island *H. jenkinsi* occurs in entirely fresh water—for example, in the burns of Bankhead, Skarrataing, Maeshowe, and the mill dam at Quoys, all in communication with the brackish lochs. None of the larger fresh-water lochs contains Hydrobia except the Loch of Skaill, where it is abundant. It was suggested in connection with the distribution of this mollusc in North Uist that calcium in considerable concentration was necessary to enable it to colonize fresh water, but in Orkney all water has a high calcium content, yet *H. jenkinsi* is not universally present, suggesting that calcium is not the only factor involved. When the mollusc first made its appearance in Orkney is not known; but as neither Scott (1890) nor Waterston (1903) mentions its occurrence, although they both collected Neritina, it is reasonably certain that it is a recent colonist. It was first reported by Oldham (1927), who found it in enormous numbers round Bridge of Brogar.

Peringia ulvæ.—The distribution of Peringia in the Loch of Stenness is peculiar. Not a single specimen was obtained from the shores of the loch, although in similar lochs in North Uist it occurred right into the shallow water; but dredging in any part produced thousands, especially where there was weed on the bottom. The shells are of large size, those of 9 mm. in length being common, and show no signs of erosion. For Peringia salinity cannot be the limiting factor here, because in North Uist and elsewhere the mollusc occurs between the salinities of 10 and 34 parts per thousand. Outside the Loch of Stenness it is absent from the Bush and various small estuaries in other parts of the island.

Neritina fluviatilis.—These two lochs are the only places in Scotland where this mollusc has established itself, and it was first recorded there by Edward Forbes (Jeffreys, 1862). Elsewhere in Britain it does not occur in brackish-water, but is common in streams and canals throughout the greater part of England and in calcareous districts in Ireland. It is absent from Devon, Cornwall, Cumberland, and wherever in fact the water is particularly soft. Typical figures for the calcium content of streams inhabited by Neritina are 20 to 30 mg. per litre (Boycott, 1936). On the Continent a dwarf race occurs in the Baltic between the salinities of 2 and 15 parts per thousand, but is prevented from penetrating into fresher water by the prevalent low temperatures, its limits of distribution coinciding with the isotherm of 13° C. In the Gulf of Finland it does not occur in water below 6 parts per thousand salinity; in the Gulf of Bothnia, where the winter temperature is higher, it is found in water as low as 2 parts per thousand salinity; in Randersfjord it occurs in water of 0·2 part per thousand salinity. In addition to this dwarf race a normal sized one occurs in most of the rivers flowing into the Baltic. Ellis (1925) gives the average length of the English specimens as 11 mm.; those in the Loch of Harray average 9 mm., those in the Loch of Stenness 6·5 mm., showing again the dwarfing effect of the more brackish environment.

It is curious that in Orkney Neritina should not have penetrated into any of the streams flowing into the lochs. This again may be a question of temperature, as all the streams are small and shallow and therefore subject to freezing in winter. Tomlinson (1936) has shown that the severe winter of 1935 caused the death of enormous numbers of Neritina in the Loch of Harray.

Mya arenaria.—This lamellibranch occurs as a dwarf form in large numbers among the weed at the bottom of the Loch of Stenness and also in the bare muddy patches. None of these individuals exceeds half an inch in length, but larger specimens up to 2 in. in length occur among the marginal weed; with a more efficient dredge larger specimens would probably have been obtained. Mya is the only bivalve present in the loch. A giant race of *Cardium edule* L. (Winckworth, 1928) occurs in the Bush, which makes its absence from the loch even as spat the more surprising.

SUMMARY.

The Lochs of Stenness and Harray on the mainland of Orkney are the only known stations in Scotland for *Neritina fluviatilis* L. The Loch of Stenness has a salinity varying between 9 and 26·8 parts per thousand; 24 species of invertebrates live in the loch, as well as several kinds of fish. The distribution of *H. jenkinsi* Smith and *Peringia ulvæ* Pennant is peculiar and only partly explicable by the salinity. The Loch of Harray is almost fresh and only slightly affected by spring tides, the salinity varying between 0·6 and 4·3 parts per thousand. Twenty-seven species of invertebrates are to be found in it, most of which are fresh-water species. The calcium content of the lochs varies from 56 to 139 mg. per litre.

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(*Issued separately August* 22, 1938.)

XIV.—The Association of Non-homologous Chromosomes in Corixidæ (Hemiptera-Heteroptera). By **H. D. Slack**, Ph.D., Assistant in Zoology, University of Glasgow. (From the Institute of Animal Genetics, University of Edinburgh.) *Communicated by* Professor F. A. E. CREW, M.D., D.Sc. (With One Plate, Nine Text-figures, Three Diagrams.)

(MS. received February 28, 1938. Revised MS. received June 4, 1938.
Read July 4, 1938.)

INTRODUCTION.

KARYOLOGICAL studies on spermatogenesis in species of aquatic bugs of the family Corixidæ have brought to light several examples of an unusual type of chromosome behaviour during the course of meiosis. It is considered to be an association of non-homologues in a manner unexampled in other animal species.

Prokofieva (1931, 1933) has described spermatogenesis in Corixidæ, giving a detailed account of one species, *Corixa distincta* Fieb., and comparing eleven other species of *Corixa*, *Callicorixa*, and *Macrocorixa*. In extending this study of the Corixidæ non-homologous association was found in species not described by Prokofieva. The nature and effect of this association on the chromosomal changes during the first meiotic division form the subject of this paper.

MATERIAL AND METHODS.

Testis preparations have been examined of Scottish specimens of the following species of Corixidæ:—

Genus *Corixa* Geoff. (*Macrocorixa* Yatsch.): *C. punctata* Illiger (*geoffroyi* Leach), *C. dentipes* Thoms.

Genus *Sigara* Fab. (*Corixa* Geoff.): *S. linnæi* Fieb., *S. striata* Fieb., *S. distincta* Fieb., *S. fallenii* Fieb., *S. castanea* Thoms., *S. semistriata* Fieb., *S. fabricii* Fieb., *S. fossarum* Leach, *S. scotti* Fieb., *S. carinata* Shlb., *S. germari* Fieb.

Genus *Callicorixa* White: *Ca. præusta* Fieb., *Ca. wollastoni* D. & S., *Ca. caledonica* Kirk., *Ca. concinna* Fieb.

Genus *Glænocorisa* Thoms.: *G. cavifrons* Thoms.

Genus *Cymatia* Flor.: *Cy. bonsdorffi* Shlb.

To obtain all stages in spermatogenesis, males in the last nymphal instar and early imaginal state were dissected in Ringer-Locke physiological saline and the testes fixed immediately after removal. Fixation for eight hours in Allen's Picroformol A3 or Langlet's Navashin mixtures gave consistent and satisfactory results for the meiotic phases of spermatogenesis. Where fixation of the pre-meiotic spermatogonial phases was desired, two hours in Langlet's Navashin or La Cour's 2BE was found to be preferable.

Sections were cut 20 micra in thickness after double embedding by the method of Peterffi (1924) and were stained by Newton's Gentian Violet method. Smear preparations stained with Zirkle's Aceto-carmine and Feulgen technique were used to assist the analysis of special structures.

DESCRIPTION.

Of the twenty species examined, *Corixa punctata*, *Sigara carinata*, and *Cymatia bonsdorffi* were found to have the paired autosomes and sex chromosomes associated non-homologously during the first meiotic division. This condition was seen particularly well in *C. punctata* and will be described in detail in this species.

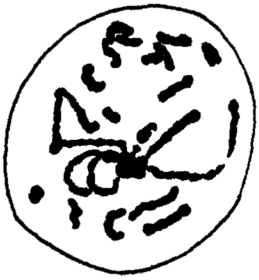
FIG. 1.—Pre-meiotic prophase showing polarisation and somatic pairing.

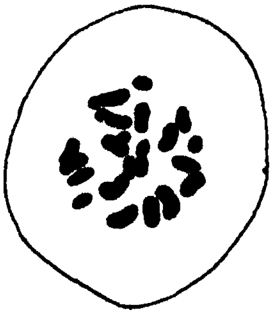
FIG. 2.—Pre-meiotic metaphase showing somatic pairing.

In Corixidæ spermatogonial divisions take place in the last nymphal instar (Prokofieva, 1933), but in *C. punctata* this phase is not complete until early imaginal life. Nuclei at the apices of the tubules of young adults still show spermatogonial divisions. An accurate analysis of these divisions was rendered uncertain by the difficulty attending satisfactory fixation. Several phases of the pre-meiotic division have been observed. Prophase stages show the diploid number of chromosomes as irregular threads of which the longer tend to be polarised at a condensed body (text-fig. 1).

This condensed body seems to represent the large nucleolus combined with the precocious X and Y chromosomes, later seen to be characteristic of the first meiotic division. As the chromosomes spiralise they contract to short thick rods, the larger elements being slightly curved. The diploid number ($2n$) of chromosomes is now shown to be twenty-four, there being twenty-two autosomes and the X and Y chromosomes. This number is characteristic of the Corixidæ. At present there is only one known departure from it, the exceptional species being *Cymatia bonsdorffi* with $2n = 26$. Contraction reaches its maximum at metaphase where there is a tendency for pairs of chromosomes of similar size and shape to lie together (text-fig. 2). Such distribution on the metaphase plate is an indication of somatic pairing of the homologous chromosomes. Somatic pairing during mitotic metaphase has been found in various Diptera, *e.g.* in *Drosophila* (Metz, 1916) and *Culex* (Moffet, 1936). The pairing in *Culex* is so close that the homologous chromosomes were mistaken by Taylor (1914) for sister chromatids and led her to an erroneous interpretation of the spermatogonial divisions. In *Drosophila* also, Stern (1931) demonstrated "somatic crossing-over" genetically, involving reciprocal exchange of segments between homologous chromosomes. From the behaviour during mitotic metaphase in *C. punctata* it seems that the homologous chromosomes tend to associate, but the case for somatic pairing cannot be more clearly defined than this owing to the small size and strong contraction of the chromosomes. Indications of a similar apposition of homologues which might be regarded as somatic pairing may also be seen in figures given by Prokofieva (1933) of spermatogonial metaphase in *C. dentipes*.

In the resting nuclei of the primary spermatocytes about twelve chromatic aggregates appear which are scattered within the nucleus at random. These bodies have been termed "pro-chromosomes" in *C. distincta* by Prokofieva (1931) and in *Lygæus* and *Oncopeltis* by Wilson (1928), and, as they correspond in number to the haploid complement, may represent parts proximal to the centromere (Geitler, 1934) of chromosomes which are already closely apposed. Some of them may represent *anlagen* of attraction centres (see below) or nucleolar material. They have a wide variation in size and form, ranging from subspherical bodies to oblong masses and short thick threads, which even at the earliest stage observed show a few fine thread-like connections. With increase in the size of the nucleus these bodies elongate to irregular threads with an anastomosis of finer filaments. In the centre of the resting nucleus lies the large nucleolus already referred to, distinguished from the rest of the complement by its lower staining power. Attached to one side of this nucleolus is a chromatic body larger than the other "pro-chromosomes." This characteristic configuration represents the nucleolus and the sex bivalent seen to be in association throughout the prophase of the first meiotic division.

Increase in size of the nucleus and cell continues until it is approximately twice that of the earliest phase of the resting stage. At the same time the presence of a haploid complement of paired chromosome threads becomes increasingly evident. The chromosomes are seen as slender threads, paired throughout the greater part of their length and in which it is possible to determine similar chromomeres in apposition. Where the chromosome ends are free they can be seen to bear terminal knoblike enlargements of chromatic material. As a rule few free ends occur, since all nuclei at this stage show a marked degree of polarisation of a peculiar form (text-fig. 3). All or most of the bivalents are intimately united either by their ends or by their sub-terminal regions. In exceptional cases an apparent lateral union by a very fine thread occurs, but this is not typical in character and is probably due to fixation. They exhibit, therefore, a property of non-homologous association of specific parts of the chromosomes.

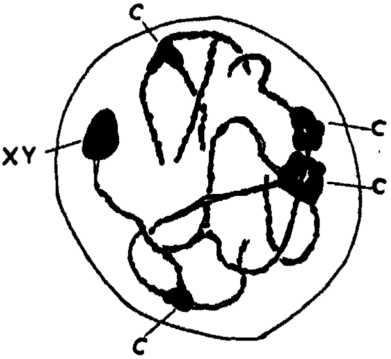

FIG. 3.—Meiotic prophase at end of zygotene stage. *c* = attraction centre. (Autosomes partially represented.)

For the purpose of discussion, there being no fundamental difference between the two classes, the types of association may be arbitrarily classified into—

(*a*) attraction centres, where the ends of more than two bivalents are polarised at one point;

(*b*) junctions, in which the ends of two bivalents are associated by a terminal or sub-terminal union.

The extent to which these structures are artefacts cannot be precisely stated, but that they are no more so than the chromosome threads is evident, since they are present irrespective of the type of fixative used in preparing the material. On the other hand, some differences due to technique exist which may be used to analyse the nature of the associations.

With fixation by Langlet's Navashin or Allen's Picroformol A3 and Gentian Violet staining, the attraction centres and junctions appear to be the union of the ends of bivalents by means of a ring-shaped or solid mass of chromatic material. At the end of the zygotene stage the material constituting these masses stains intensely, throwing the centres into strong relief (text-fig. 3). Later, as the chromosomes contract and thicken, their staining becomes more like that of the centres, and the difference is lost.

Material fixed for two hours in Langlet's Navashin mixture and stained by Feulgen's method gave precisely similar results as with Gentian Violet, the chromosomes and uniting material being stained to the same extent. Treatment of smear preparations with Zirkle's Aceto-carmine reveals in greater detail the structure of these associations, and it is seen that each chromosome end bears the rounded knob referred to above, which is fused with that of any chromosome other than the partner homologue. For example, in an attraction centre comprising four bivalents, the ends of the homologous chromosomes A′ and A″ are associated with those of the neighbouring chromosomes B′ and C′; while B″ and C″ are similarly associated with the ends of the fourth bivalent D′ and D″ in the manner illustrated in the diagram (diagram 1, Plate (*a*)). Junctions may take the form of end-to-end contacts or the association of one end of a bivalent with the sub-terminal region of another which also appears to possess an aggregation of chromatic material. Only one sub-terminal region having this property occurs in a single bivalent.

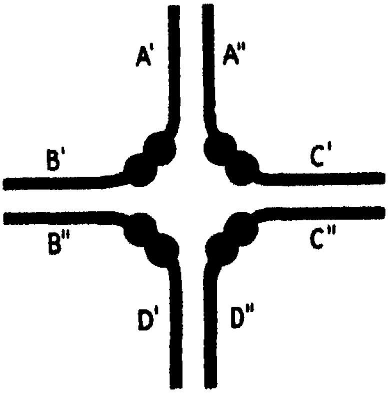

DIAGRAM 1.—The structure of an attraction centre involving four bivalents.

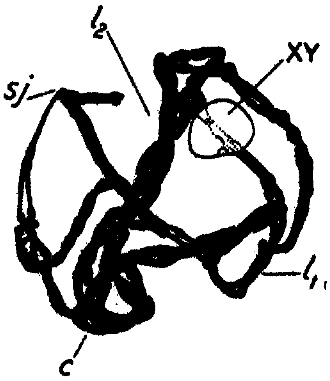

FIG. 4.—Meiotic prophase at early diplotene.
l_1 = simple loop bivalent.
l_2 = interlocking loop bivalents.
sj = sub-terminal junction.
(XY in outline.)

Non-homologous attraction characterising meiosis of *C. punctata* results in a variety of configurations in the prophase nucleus. In the simplest form one end of a bivalent may make contact with an end of a second, opposite ends in each case being free, but generally structures of greater complexity are found. One bivalent may be polarised at each end at two centres or at the same centre. If polarised at two centres it may also be associated at a sub-terminal point with the end of a second bivalent. Two or more bivalents may unite into a chain by simple junctions and the ends of the chain enter attraction centres. When both ends of a bivalent or chain of bivalents enter the same centre a loop is formed (Plate (*b*)) which frequently interlocks with a similar loop polarised at a second centre. Text-fig. 4 and diagram 2 illustrate the different types of association observed. A small nucleolus occurs on one bivalent in an interstitial position, and at late pachytene may be found free in the nucleus. The bivalent bearing it is thus recognisable, and its behaviour may be followed. In most cases this bivalent forms associations by simple junctions, and in one nucleus by an attraction centre and a junction; but in no instance does the interstitial nucleolus fuse with the uniting material developed by other bivalents, since interstitial associations have not been found.

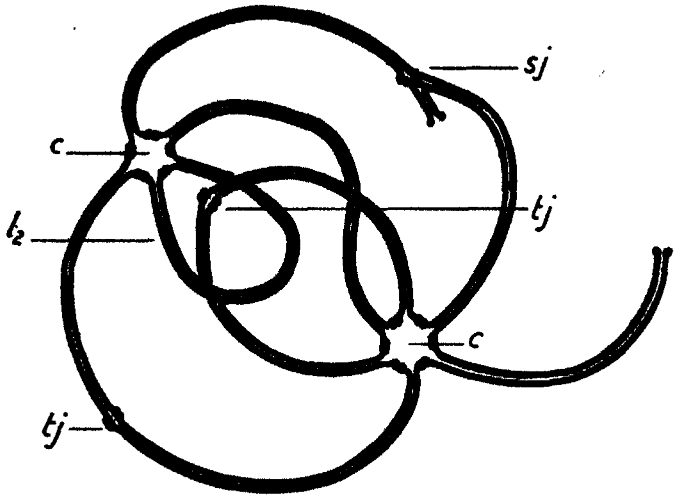

DIAGRAM 2.—Diagrammatic representation of the different types of non-homologous association. (Lettering as in figs. 4 and 6.)

TABLE I.

		No. per Nucleus of Attraction Centres, Junctions, and Free Bivalent Ends :—											
		0.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
No. of nuclei with each class of	Attraction centres	0	1	8	10	3	1	0	0	0	0	0	0
	Junctions . .	3	8	6	2	1	2	1	0	0	0	0	0
	Free bivalent ends	0	0	1	7	6	3	1	3	1	0	0	1

Table showing segregation of 23 nuclei into classes having different numbers of attraction centres, junctions, and free bivalent ends at pachytene and early diplotene stages.

Table I illustrates the extent of polarisation and non-homologous union, though allowance must be made for error arising from the low number of nuclei on which it is based. The degree of polarisation varies but is generally well developed. In all nuclei at least one attraction centre occurs, the frequency in each nucleus ranging from one to six and showing a modal value of three. Since the mode coincides with the mean a random distribution of the numbers of centres is indicated. The frequency of junctions is correspondingly low, 60 per cent. of the total number of nuclei examined having one or two such associations. This refers to both end-to-end and sub-terminal relationships, the latter having a frequency of 43 per cent. for one sub-terminal junction and 4 per cent. for two, in individual nuclei. Loop bivalents were found in 70 per cent. of the nuclei examined.

Where bivalents remain unpolarised, either wholly or partially, the distribution of the different numbers of free bivalent ends given in Table I shows their frequency. This distribution, which does not include short free ends in cases of sub-terminal contact, reaches a major peak of 30 per cent. for nuclei with three free ends, and minor peaks for those with seven and eleven.

Orientation of the centres is not entirely random. They tend to take up a peripheral position close to the nuclear membrane. When two centres occur they usually lie at opposite sides of the nucleus, and when three are present their loci are separated by approximately one-third of the circumference of the nucleus.

The XY bivalent is free from association in about 70 per cent. of the nuclei, but otherwise forms an attraction centre with one or more autosomes. The striking dissimilarity of this bivalent from the autosomes, engendered by its precocious condensation and close association with the large nucleolus, makes it the most outstanding body in the prophase nucleus.

It is possible to determine the structure of the sex bivalent during pachytene due to the progressive opening out of the condensed mass taking place through the relaxation of the intimate association with the nucleolus, similar except for its precocity to the behaviour of the autosomes at the diplotene stage. In the typical form two sub-terminal chiasmata are found in short pairing segments separated by a long intercalary differential segment in both X and Y (text-fig. 5, diagram 3). The two chromosomes differ but little in length, though the X is recognisably the longer. When autosomal attachments occur they are located close to one chiasma. In many nuclei this typical form of the XY is obscured, apparently owing to the effect of the fixative on the degenerating nucleolus, whereby it condenses into an irregular network of strands connecting the two chromosomes.

One chiasma may become terminal before the end of pachytene, but the time at which this occurs varies and it may not take place until early, or even late, diplotene stage. The terminalisation of one chiasma before the other is characteristic, and is probably that of the short arm. Types may be found in which no chiasma forms at one end; and in exceptional instances pairing appears to have failed entirely, the nucleolus alone serving to hold the X and Y together.

The nucleolus generally disappears during the opening out of the sex bivalent, remaining longer in atypical figures where pairing is incomplete. The heteropycnosis of the XY and large size of the nucleolus in which it appears to be embedded retards the rate at which extension and opening out of the differential segments proceeds in relation to the autosomal changes.

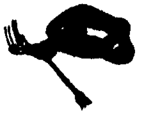

Fig. 5.—XY bivalent at diplotene with attached autosomes.

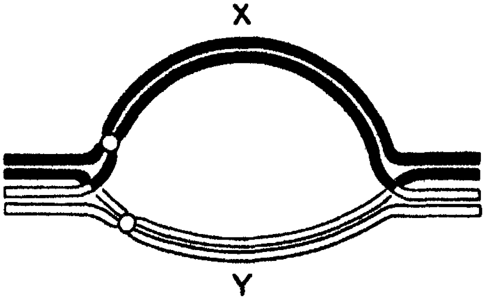

Diagram 3.—Normal pairing of XY bivalent.

During the pachytene stage the nucleus undergoes synizesis and passes into a phase where fixation fails to preserve the normal structure of the chromosomes. They clump together and cannot be clearly distinguished. Because at all other stages the chromosomes do fix satisfactorily, such a failure suggests the occurrence of active physico-chemical changes within the nucleus at this time.

With the onset of diplotene a progressive opening out of the loops in the paired homologous autosomes commences owing to repulsion between them. Relational coiling between the chromosomes of the individual bivalents can be clearly recognised when this occurs (text-fig. 6; Plate (*d*)). With few exceptions all the autosomal bivalents are seen to be relationally coiled. The degree of coiling does not seem to show any direct relationship to the length of the bivalent. Both long and short chromosomes frequently show the same amount in the same nucleus. Free bivalents do appear to show a greater degree of coiling relative to their length than those which are completely polarised, and this also applies to those with one free end. In some cases coiling is not consistently developed throughout the length of a polarised bivalent, but fails towards one end, and finally instances occur where relational coiling and interstitial chiasma formation are absent, pairing being maintained only at the ends. Though coiling may be determined it has not been possible to demonstrate in all cases at this stage the difference between simple passage of one chromosome over its partner and actual chromatid crossing-over between the two.

A second kind of coiling has been observed where two re-entrant or loop bivalents interlock (see p. 197), (text-fig. 6). If these are polarised at diametrically opposite centres and are pulled out owing to their combined length, being approximately equal to the distance between the poles (*i.e.* attraction centres), then a further coiling may take place between the two arms of the looped bivalent. This is opposite in direction to that of the relational coiling. It bears a resemblance to the doubling back and coiling of the univalent inert B chromosomes observed in polysomic complements of *Zea mays* (McClintock, 1934) and in salivary gland chromosomes of *Drosophila* (Koller, 1935). In this case the doubling is of a bivalent, and the coiling may be an expression of unsatisfied tension produced by the combined effects of relational coiling and the attachment of the ends at attraction centres.

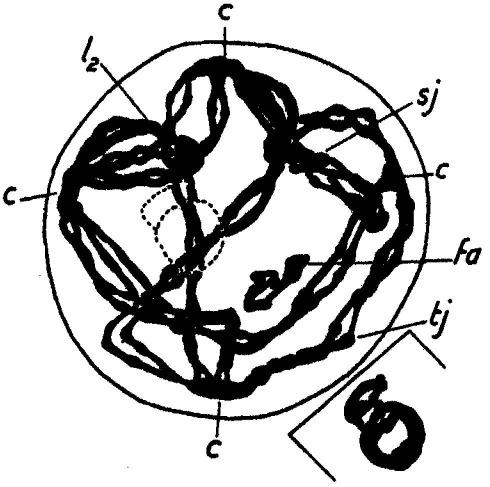

FIG. 6.—Meiotic prophase at mid-diplotene. *fa* = free autosome. *tj* = terminal junction. Other lettering as in fig. 4. (Insert XY and remains of nucleolus.)

At later diplotene stages the polarised bivalents enter into a phase in which progressive liberation from attraction centres and junctions takes place. This breaking up of the association complex is not usually completed until metaphase. The number of free bivalents at each stage of the first meiotic division given in Table II illustrates this process.

At pachytene and early diplotene the numbers of free bivalents represent those which have never been associated with the polarised elements in the nucleus. From mid-diplotene to late diakinesis the increase in mean number of free bivalents per nucleus indicates a rapid release of the individual bivalents until, at prometaphase, most, and at metaphase all, of them are free. The mechanism which brings about this separation of the haploid complement into its components is that which normally operates in the nucleus during the passage from diplotene to metaphase.

TABLE II.

Stage.	(*a*) Mean No. of Free Bivalents per Nucleus.	(*b*) Mean No. of Free Sex Bivalents per Nucleus.	(*c*) No. of Nuclei Counted.
Pachytene and early diplotene	1·182	0·727	11
Mid-diplotene	1·477	0·762	21
Late diplotene	4·771	0·690	23
Early diakinesis	7·800	0·600	10
Diakinesis	8·936	0·886	19
Prometaphase	11·484	0·954	16
Metaphase	12·000	1·000	20

In the first place internal spiralisation, now actively taking place, contracts the chromosomes until, at metaphase, the length has been reduced to approximately one-seventh of that at diplotene shortly before any liberation of associated elements occurs. Secondly, the mutual repulsion of paired homologues and attraction centres, already seen at pachytene and early diplotene, still continues. These two forces, the one internal, the other external, act concurrently to draw away the associated ends of bivalents from one another. As they separate the material forming the union is drawn out into fine threads. Each chromosome is seen to connect with a non-homologous chromosome of another bivalent by one thread, while no such connection exists between homologous partners. Once one end of a completely polarised bivalent or chain of bivalents is freed from an attraction centre, contraction can play no further part in causing separation of the units from the remaining centre and junctions, if the latter be present. Two further forces are brought to bear on the associated complex. These are the repulsion forces acting between the bodies of homologous partner chromosomes and between their centromeres. At a late phase of the diplotene stage, in bivalents having more than one chiasma, interstitial loops widen and assist in shortening the distance between the ends. Distal ends possessing no terminal chiasmata tend to separate, as do ends having terminal or sub-terminal centromeres. Under the influence of these forces the threads joining non-homologous chromosomes are stretched still further and ultimately break, freeing the bivalents from their associations. Complete dissociation is not achieved at once. Frequently the first to break is one thread of the union between two bivalents, leaving the second joining thread intact. This type of breakage is found in the liberation of bivalents having unpaired end segments strongly repulsed, and the remaining connection persists until broken by the mutual repulsion of all bivalents, which completes the diakinesis stage. Terminal or sub-terminal chiasmata allow the connections between both pairs of chromosomes of two bivalents to exist until a later stage by preventing this separation of homologous end segments. This is well shown in the association of the XY bivalent with an autosome. Here the sub-terminal chiasmata of the XY allow no separation of the ends, and connection with the autosome may endure longer than any other non-homologous association, as may be seen from the frequency of free sex bivalents (Table II), at successive stages where the sudden rise does not commence until early diakinesis.

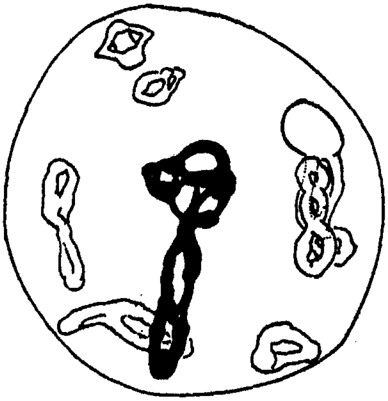

FIG. 7.—Late diplotene. Complex union of four bivalents due to non-homologous association.

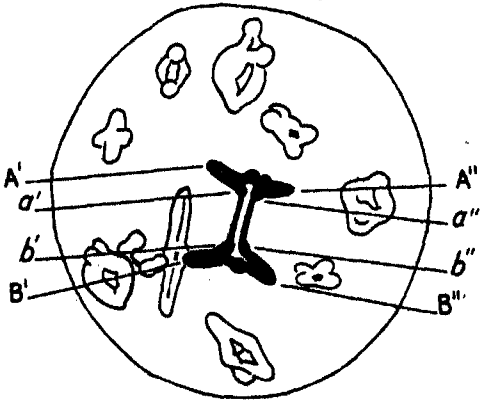

FIG. 8.—Early diakinesis. Partial breakage of a chiasma due to separation of fused homologues. (For explanation of lettering, see p. 203.)

At late diplotene instances of false interlocking occur where one bivalent passes through the loop formed by the opening out of the partner chromosomes of another. It probably took place at an early stage before the completion of pairing when strong repulsion forces were not operating to prevent the interlocking. Fixation of the bivalents at attraction centres would subsequently play a part in maintaining the positional relationship.

In several nuclei an association of four bivalents seems to depart from the rules governing non-homologous associations observed by all other complements examined. Three of these bivalents are united by chromatic threads in a manner which can only be analysed as a union of one chromosome with the chromosomes of two other bivalents by a double thread (text-fig. 7). The interpretation of this configuration is rendered difficult by the combination of terminal and sub-terminal associations and the contraction of the chromosomes.

In some nuclei the union of non-homologous chromosomes occasions the partial breakage of chiasmata (text-fig. 8). Here the ends of chromatids *a'* and *a"*, of partner chromosomes A', A" are united with the ends of chromatids *b'* and *b"* of another pair B', B" by separate strands. Repulsion of the bivalents has set up sufficient tension in the connecting strands to cause the breakage of the homologous association of these chromatids at the chiasmata. It is important to note that in this case chromatids and not whole chromosomes are united by separate strands in the non-homologous union. From this structure it may be inferred that the association of non-homologous chromosomes, so far seen to be effected by single chromatic strands, is in reality an association of individual chromatids. If this view be taken, each chromosome is connected by two parallel strands as a result of division of the homologues into daughter chromatids. This may well have occurred if the two bivalents were closely approximated at the time and the uniting material condensed into a compact mass, repulsion of the bivalents then drawing it out into a pair of strands. Such behaviour indicates a further character of the uniting material, namely, that it has a predetermined cleavage plane along the axis joining its points of contact with the non-homologous chromosomes. In a few instances bivalents seem to show this partial breakage of a chiasma after the lapse of non-homologous union at metaphase.

During diakinesis the bivalents show maximum repulsion and lie for the most part near the nuclear membrane.

At this stage non-homologous association has relaxed until only two elements remain united as a rule, but occasionally three or four are still conjoined. All members of the complement have now contracted to a marked extent, and appear as short rods, crosses, or rings, according to the number and degree of terminalisation of chiasmata. Contraction is accelerated from diplotene onwards in the autosomes relative to that in the sex bivalent, which becomes difficult to recognise in many nuclei as its former precocious contraction now no longer serves as a distinguishing character.

In some preparations with optimum fixation and staining the position of the centromeres and their relation to chiasma distribution can be determined. The product of advanced contraction and strong repulsion of the sub-terminal centromeres in certain autosomes forms a characteristic structure. The short proximal arms of these chromosomes, represented by minute spherical bodies, are drawn away from the long arms and remain separated by thread-like constrictions. The resultant structure bears a close resemblance to a trabant. The position of this structure varies according to chiasma distribution. Where the chiasmata are in the long arms the "trabants" stand at opposite ends of the terminalised bivalent (text-fig. 9 (*a*)). A chiasma in the short arms (*i.e.* in the "trabants") brings them together, so that they are placed on an axis perpendicular to that of the long arms (text-fig. 9 (*b*)). In a few instances terminal non-homologous association still remaining between the short arms of two or more bivalents may be seen to draw out the constrictions to a length equal to that of the remainder of the bivalent (text-fig. 9 (*c*)). At the prometaphase, when formation of the spindle and congression of the bivalents at the equator of the cell take place, very few cases of bivalents remaining in connection have been found. Occasionally two or three are still linked by fine threads and appear to be retarded in their movement towards the equatorial plane in consequence.

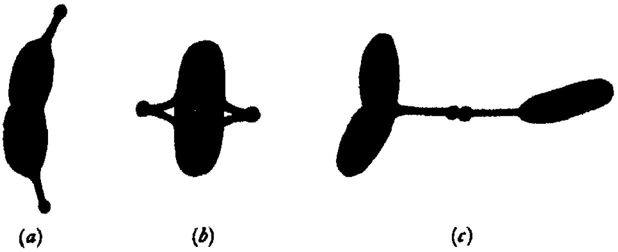
(*a*) (*b*) (*c*)

FIG. 9.—Bivalents at diakinesis showing "trabants."
(*a*) Chiasma in long arm.
(*b*) Chiasma in short arm.
(*c*) Non-homologous fusion of short arms.

The first meiotic metaphase which follows this stage marks the final disappearance of any indication of non-homologous association of the chromosomes in *Corixa punctata.*

In all other species of Corixidæ of which the pachytene and early diplotene stages have been examined, attachment of the bivalent XY to one or more autosomal ends has been found (Plate (*f*)). The percentage frequency of this attachment varies from 12 per cent. of the nuclei in *Sigara fabricii* to 81 per cent. in *Callicorixa concinna.* There is also a marked tendency for high frequencies of XY attachment to be correlated with an increased number of autosomal ends to which the sex bivalent is attached.

Additional evidence of the non-homologous association of autosomes not involving the XY has been found in only two species other than *C. punctata*. In *Sigara carinata* and *Cymatia bonsdorffi* pachytene and diplotene nuclei bear a close resemblance to the equivalent nuclei of *C. punctata* with respect to the appearance of attraction centres (Plate (*e*)); but the phenomenon in these two forms has not yet been studied in detail.

DISCUSSION.

In the maturation divisions of the male germ cells of *Corixa punctata* two phases of the first meiotic division have not been observed. The chromosomes appearing during the early stages in the development of the primary spermatocytes never at any time had the appearance of a diploid set of single threads. Their first appearance as clearly defined threads is at late zygotene stage when pairing is nearly complete.

In the light of the evidence of a tendency to somatic pairing during the pre-meiotic spermatogonial division, it is probable that attraction is exhibited by the homologous chromosomes in a precocious degree so that they segregate in close proximity at anaphase. Thus the homologues would be closely apposed at the ensuing resting stage. Such behaviour might well result in the elimination of visible leptotene and early zygotene stages and ensure pairing at meiosis.

The most striking feature of meiosis in *C. punctata* is the non-homologous association of chromosomes and its persistence throughout the greater part of the first meiotic division.

The enlarged chromosome ends at late zygotene and early pachytene resemble the "polar granules" of *Phrynotettix* (Pinney, 1908; Wenrich, 1916), which may also fuse together, and which Wenrich describes as expanding to form "vesicles" or "plasmosomes." Corey (1933, 1937) observed fusion of chromosome ends in a number of Orthopteran genera. In all these cases the result of fusion is to form large irregular chromatic masses, and union of non-homologues only lasts until the early diplotene stage.

Darlington (1936) suggests that fusion of non-homologous chromosome ends is conditioned by the presence of nucleolar material. This implies that in the case of *C. punctata* all the chromosomes develop, or may develop, nucleoli of which the organisers are terminal or sub-terminal in position. The enlargement of the free ends of chromosomes to form knobs agrees with this idea. They may possibly represent aggregates of nucleolar material which have failed to fuse in competition with the aggregates of the successful attraction centres.

The behaviour of the XY complex, both in *C. punctata* and in other species, also upholds the theory of nucleolar fusion and is probably its strongest support. When the sex bivalent has attached autosomes its extension and opening out does not as a rule take place until the autosomal association lapses at diplotene, and the bivalent remains until then in the condensed mass characteristic of the earlier phases. This breaking of the fusion of the autosomal connection with the sex bivalent is not necessarily to be regarded as a trigger mechanism instigating further development of the XY complex, but may be considered an expression of the dissolution of nucleolar material which by liberating the chromosome elements allows extension to take place (Darlington, 1936). It is necessary to decide in this case whether the liberation of the autosome occurs independently of the liberation of the XY from the nucleolus or whether both are a function of the dissolution of the nucleolus. Since the general procedure seems to be for the nucleolus to disintegrate in advance of the autosomal liberation, it may be concluded that it is an independent process which collaborates with the non-homologous union to bring about the delay in the opening out of the XY.

The evidence provided by the application of Feulgen's technique (p. 196) is certainly contrary to the hypothesis that nucleolar material is responsible for the union of non-homologues. This reaction seems to be the most reliable microchemical test for the presence of thymonuclein, and although instances are known where chromosomes do not give a positive result while the nucleoli do (*e.g.* "lampenbürsten" chromosomes of certain growth stages of egg-nuclei of *Salamandra* are negative and nucleoli of growing eggs of *Stegomyia* are positive with respect to Feulgen technique (Hartmann, 1933)), it may generally be assumed that nucleoli do not stain by this process. As already stated, both the chromosomes and the material uniting their ends gave positive results, and the latter on these grounds cannot be accepted as nucleolar in nature. Furthermore, the material uniting non-homologues persists up to metaphase and is stretched out under the influence of chromosome repulsion at late diplotene, whereas nucleoli disintegrate at an earlier stage. Some difference must exist, therefore, between this uniting material and the material of nucleoli.

In notes on the heterochromatic chromosome ends of *Crepis*, Kostoff and Arutinian (1938 *a* and *b*) have drawn attention to the property of heterochromatic inert regions to form non-homologous associations shown to be true in the case of *Drosophila* by Prokofieva-Belgovskaya (1935). In the salivary gland nucleus of *Drosophila* the centromere regions of the chromosome pairs are heterochromatic and fuse together to form a chromocentre. Bauer (1936) regards the heterochromatic material as consisting of modified chromomeres, "heterochromomeres" differing from the "euchromomeres" in their reaction to nuclear dyes. To these heterochromomeres he accords the special property of non-specific attraction. Moreover, Bauer postulates a non-specific affinity of terminal chromomeres in these chromosomes which exist in a condition of permanent prophase. The application of similar properties to the chromosomes of *C. punctata* offers another explanation of the attraction between non-homologues. Association at centres and end-to-end junctions may be a function of Bauer's "non-specific affinity of terminal chromomeres," and sub-terminal junctions a function of "non-homologous attraction of heterochromomeres." In this respect it may be pointed out that all the observed types of association can be analysed as being the union of two, and only two, non-homologous chromosomes at one point (analogous to pairing in polyploids with homologous segments). This is illustrated by the characteristic ring formation of centres concerning four or more bivalents (diagram 1).

McClintock (1933) described knobs of deeply staining material on the prophase chromosomes in pollen mother-cells of *Zea*, and Longley (1937) reported similar knobs in other grasses, namely, *Euchlæna*, *Euchlæna-Zea* hybrids, and *Trypsacum*, and observed their fusion to produce non-homologous associations. Longley suggests that these knobs are large chromomeres, and also concludes that they represent inert regions of the chromosomes which possess the power of sticking together. The association of many chromosome ends bearing knobs results, however, in a large undifferentiated mass, and does not seem to produce the ring-formation characteristic of the uniting material in pachytene chromosomes of *Corixa punctata*. Non-homologous association in *C. punctata* appears to be regulated by a special type of behaviour which does not govern the similar association in *Euchlæna* and its allies.

Several factors may contribute to bring about the condition observed. It may be a secondary reaction due to, or at least facilitated by, a primary polarisation such as occurs in *Chorthippus* and *Stethophymia* (Janssens, 1924). A primary attraction centre bearing perhaps some relation to the centrosome, as Darlington (1936) suggests, which causes an accumulation of all bivalent ends to one point in the nucleus, would enhance the formation of secondary associations of these ends by fusion. At the same time the possibility of interstitial associations taking place would be reduced, and this accords with the evidence. The observed phenomena of polarisation in *C. punctata* give no support to this hypothesis, and, unless the occurrence of a "bouquet stage" in *C. distincta* (Prokofieva,

1931) can be admitted as evidence of an initial primary pole, it must be inferred that several centres are formed primarily in each nucleus.

It is possible that the centromeres play some part in bringing non-homologous chromosomes together. Darlington (1937) observed a tendency for centromeres to be mutually attracted in *Agapanthus* and *Stauroderus*, and suggests that this should be regarded as evidence of the essential homology of all centromeres by virtue of a common evolutionary origin rather than as non-specific attraction between them. Centromere attraction can play, at the most, only an accessory rôle in *C. punctata*, since both ends of the chromosome possess the property of fusion. It is worthy of note, however, that only one sub-terminal region has this property in any one bivalent, which suggests that it is the region of the centromere. While the fusion of a sub-terminal region with the distal end of the same bivalent has not been observed, it is to be expected that the association of sub-terminal regions of different bivalents (*i.e.* on this assumption their centromeres) should occur. This also has not been found.

Distinct from the problem of the nature of polarisation during prophase is the consideration of orientation of centres and junctions within the nucleus. Evidence in favour of some force operating on the centres is forthcoming from the behaviour of loop or re-entrant bivalents (p. 197). Where two such bivalents, associated with diametrically opposite centres, interlock, the loops are pulled out, indicating a movement of the attraction centres towards the periphery of the nucleus. It is noticeable that the peripheral position of the centres is reflected in that of the sex bivalent, and that those centres possessing the largest masses of uniting material are those which show the greatest regularity in taking up a position near to the nuclear membrane. This orientation suggests the action of an external force leading to a peripheral position of condensed elements in the nucleus. The action of an electrodynamic force (*cf.* Lillie (1905), Cannon (1923), Kuwada (1929)), in the form of a surface charge carried by the chromosomes, would tend to the mutual repulsion of all members of a complement. Here, however, the bivalents are restricted in their range of movement by the polarisation of their ends, while the attraction centres bearing large masses of uniting material might be supposed to exhibit stronger repulsion by virtue of a greater surface charge, and hence assume equidistant peripheral positions, leaving single or conjoined bivalents associated with them to be mechanically arranged within the nucleus. As in the case of the sex chromosomes, free autosomes usually show a peripheral orientation in accordance with this hypothesis.

With the separation of the bivalents and their opening out at late diplotene determination of chiasmata becomes possible.

From the determination of chiasma frequencies at successive stages from late diplotene to metaphase, unexpected results emerge with respect to the terminalisation coefficient. As is to be expected, the number of chiasmata per bivalent falls owing to terminalisation until this is complete at metaphase. The sequence of terminalisation coefficients does not reciprocate the fall in mean number of chiasmata per bivalent. From late diplotene until diakinesis the terminalisation coefficient also falls, and thereafter rises rapidly up to unity, denoting complete terminalisation at metaphase (Table III).

TABLE III.

	Xta.					No. of Cells.	Total Xta.	Total Terminalised.	Mean No. per Cell.	Mean per Bivalent.	Terminalisation Coefficient.
	1.	2.	3.	4.	5.						
Late diplotene .	17	36	4	2	0	5	107	45	21·4	1·76	0·470
Late diplotene .	22	24	1	1	0	4	77	26	19·25	1·61	0·338
Early diakinesis	82	37	1	0	0	10	159	44	15·9	1·32	0·277
Diakinesis .	85	33	1	0	0	10	156	40	15·6	1·30	0·256
Late diakinesis .	29	7	0	0	0	3	43	27	14·33	1·19	0·627
Prometaphase .	32	3	0	0	0	3	38	38	12·66	1·05	1·000

Throughout these phases in the first meiotic division separation of non-homologously associated bivalents is taking place. Before separation many chromosome pairs may appear to have terminal chiasmata owing to their ends being closely held together by the tension in the material uniting them to other bivalents. As each bivalent breaks free, centromere and body repulsions force apart those paired chromosome ends which do not actually possess terminal chiasmata, and, so long as this process continues, the observed terminalisation proceeds in a negative direction. From diakinesis to metaphase true terminalisation is observed, and the coefficient rises in the expected manner, since the lapse of non-homologous association now allows a valid analysis.

The persistence of the union of at least two of the bivalents up to prometaphase in some nuclei leads to the inference that the final expression of non-homologous association is to be found in the imperfect formation of a hollow spindle at first metaphase, a characteristic of most members of the Corixidæ (Prokofieva, 1933). This conclusion is invalidated, however, by the behaviour of the chromosomes at second metaphase when they still fail to form a perfect hollow spindle, and by the similar conformation of both spermatocyte metaphase stages in *C. dentipes* in which non-homologous unions do not occur.

SUMMARY.

1. The study of twenty species of aquatic bugs (Hemiptera-Heteroptera) of the family Corixidæ has revealed the occurrence in *Corixa punctata*, *Sigara carinata*, and *Cymatia bonsdorffi* of non-homologous association of paired chromosomes during the first meiotic division in spermatogenesis.

The pre-meiotic and first meiotic divisions in *C. punctata* are described, showing the appearance and effects of this property of the male germ-cell chromosomes. Its possible nature is discussed. Reference is made to a similar form of non-homologous association in *S. carinata* and *Cy. bonsdorffi*, but these species have not been studied in detail.

2. In the pre-meiotic spermatogonial division of *C. punctata* there is evidence of somatic pairing at prophase and metaphase. Leptotene and early zygotene stages were not found in the following meiotic prophase of the primary spermatocyte. On these grounds it is supposed that a tendency for somatic pairing leads to the close apposition of the chromosomes when they become visible at the commencement of meiosis.

3. All nuclei exhibit a form of non-homologous association involving all or most of the chromosomes from the time of their appearance in meiotic prophase until late diplotene stage. It then commences to break up, and finally disappears at diakinesis or prometaphase, leaving free bivalents at metaphase.

4. This non-homologous association concentrates the ends of bivalents into a limited number of loci within the nucleus, and may be looked upon as a form of polarisation. It is an association of non-homologues restricted to specific parts of chromosomes which are either terminal or sub-terminal in position. It appears to be a fusion of knob-like enlargements of each chromosome resembling the "polar granules" of *Phrynotettix* and to some extent the knobs found in *Zea*, *Euchlæna*, and *Trypsacum* chromosomes. Variations in fixation and staining technique which still give satisfactory images of the chromosomes do not cause a significant change in the appearance of the non-homologous association.

5. To facilitate description the types of terminal or sub-terminal fusion have been grouped under two headings, viz. "attraction centres" and "junctions," according to whether more than two or only two bivalent ends associate at one point. Association at an attraction centre may be briefly described as being analogous to a multiple chiasma.

6. An account is given of the various configurations formed by this association and of the degree to which it extends in the primary spermatocytes. The breaking-up of these configurations by the forces operating on the chromosomes from diplotene onwards is shown to draw out the uniting material into fine threads joining the non-homologues until they finally break, leaving all the bivalents free at metaphase. The influence of this process on the apparent terminalisation of chiasmata produces an atypical sequence of terminalisation coefficients probably due to the impossibility of determining true terminalisation until the disappearance of the non-homologous fusion.

There is evidence also that relational coiling is partially interrupted by fixation of the ends of the chromosomes at the attraction centres.

7. The nature of this association is discussed and reasons given for considering it to be the non-specific attraction of heterochromatic inert regions of the chromosomes rather than the fusion of nucleolar material.

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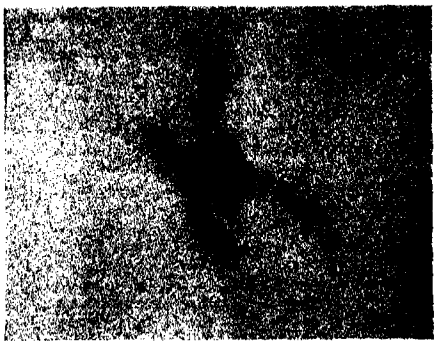
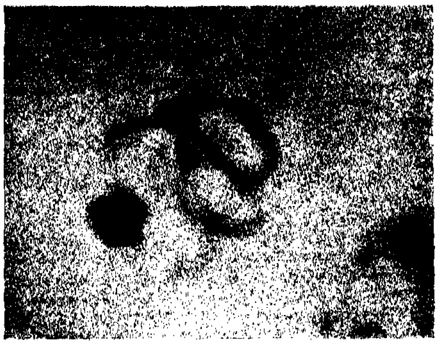
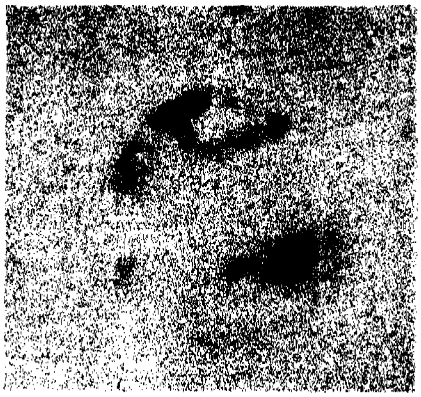


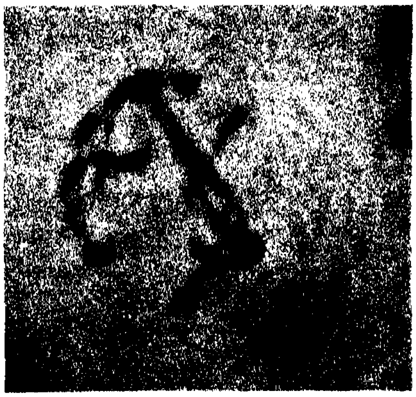
(a) *C. punctata.* Attraction centre involving four bivalents at pachytene. × 5500.



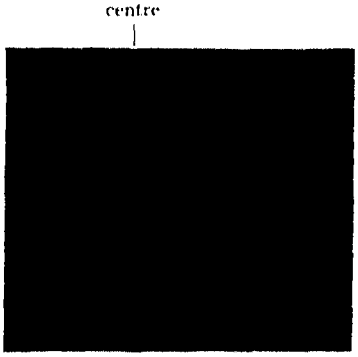
(b) *C. punctata.* Two loop bivalents entering one centre at pachytene. × 3200.



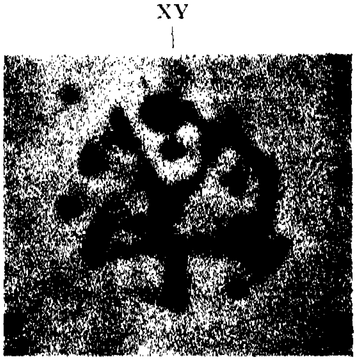
(c) *C. punctata.* Paired homologous chromosomes entering a centre at early diplotene. × 3200.



(d) *C. punctata.* One bivalent associated with two centres at mid-diplotene. × 3200.



(e) *Cy. bonsdorffi.* Attraction centres at pachytene. × 3200.



(f) *Cy. bonsdorffi.* Attachment of XY to autosome at pachytene. × 3200.

XV.—On Rare Defects in Human Populations with Particular Regard to In-breeding and Isolate Effects.

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1. INTRODUCTION.

In theoretical analyses of the hereditary composition of human populations it is often assumed that crossing occurs at random and that individuals with different hereditary make-up are equally fertile. This state of things has been called amphimixis. Sometimes such assumptions tally so closely with the actual state of things that it is possible to employ calculations carried out from this point of departure. In other cases processes present in populations cause larger or smaller deviations from amphimixis.

Of particular importance is the fact that there are within the same country boundaries across which interbreeding seldom or never takes place. A country is divided by barriers of geographic nature—for instance, forests, rivers, and so forth—into minor populations within which it is fairly justifiable to speak of amphimixis. Besides this there are also barriers of a social nature, preventing or rendering more difficult crossing between persons belonging to different social strata. Starting from this fact, we may maintain that a population is made up of minor populations, "*isolates*", within which we are fairly justified in speaking of amphimixis. In certain circumstances it is possible to ignore these boundaries, but more often it is not correct to assume that amphimixis occurs throughout the whole of the population.

The term "isolate" was first defined by Wahlund, and the significance of the isolate boundaries has from different points of view been analysed by Wahlund and by the present author. We may maintain that each separate individual has his own isolate, his own circle, within which it is possible for him to marry. For a larger or smaller group of persons these individual isolates may be considered as coinciding fairly well. An isolate is, in fact, no sharply circumscribed unity. The possibility of a marriage decreases, for instance, with geographic distance, in many cases in such a way that the isolate may be said to thin down slowly towards the remaining population. In order to get a better starting-point for calculations, however, it is suitable to conceive of the actual isolates as replaced by schematized unities of more distinctly circumscribed smaller circles within which amphimixis is considered as taking place.

Naturally it is most reasonable to suppose that rare recessive characters first arise in the form of gene mutations. A person who by mutation becomes the carrier of a gene may not happen to propagate, in which case the gene disappears. But it may equally well happen that he leaves the gene to a larger or smaller number of descendants. In this way the gene may spread to a certain extent. After several generations, through marriage of related persons, the genes may be brought together in double dose so that a homozygote arises. In practice the earliest possibility is intermarrying of first cousins. The probability of this is greater in small than in large populations, and greater in cases where intermarriage of related persons commonly occurs than when it is rare. This implies that mutations which bring with them a serious recessive defect are more dangerous in small populations than in large.

With regard to hereditary defects in general, it should be borne in mind that when the defect is serious and shows at an early stage—for instance, at birth—monohybrid dominance is as a rule out of the question. Owing to their defects the character-carriers are not able to propagate. Dominant genes of this type consequently annihilate themselves at once. In recessive heredity the situation is different. Even though the homozygotes are not able to reproduce themselves, the gene may be transmitted to subsequent generations through the heterozygote.

When trying to determine the occurrence of individuals who carry genes in latent form, we have to pay regard to the mechanism of isolates. Sjögren (1931) has carried out an approximate estimate of the frequency of heterozygotes with regard to amaurotic idiocy, and found that these cases amount to 1 per cent. of the population in Sweden. Referring to Wahlund and to Dahlberg, he emphasizes that the calculation is approximate, and that the gene is only present in certain centres among the population, not being spread all over it. In point of fact this deviation from amphimixis all over the population makes the calculation altogether misleading. A correct calculation should show that in the isolates where the gene occurs the frequency of heterozygotes is much higher than 1 per cent., whereas the number of heterozygotes as related to the entire population under these circumstances amounts to only a small fraction of 1 per cent.

A question which thus presents itself is what processes affect the frequency of characters of this rare type. It is obvious that the frequency of mutation plays an essential part, but we are not able to influence it, and we know little about it. As has been pointed out above, we may only assert that mutations in large isolates are less risky than mutations in small isolates. When it is a question of characters of this type, the policy of sterilizing character-carriers is usually advocated. In principle this is to be desired. There is certainly no reason why a seriously defective person should be allowed to leave the gene of the defect to his offspring. In this context the author cannot discuss in detail under what circumstances and to what extent such sterilization should be carried out. The object of this communication is to point out other important aspects of the problem.

It has been shown that, when applied to very rare genes, sterilization of character-carriers has no real effect on the population. The first scientist to give an extensive analysis of the problem from a mathematical point of view was J. B. S. Haldane (1923–32). The present author also, without at that time knowing about Haldane's work, advanced formulæ for the effect of selection and discussed their significance for human populations. (I wish to mention this here, because Haldane's work, which was published in a journal of limited circulation, is not referred to in my earliest publications.) Such mathematical analysis postulates genes which show a specified frequency, it being assumed that the character-carriers themselves are prevented from propagation. It then appears that this brings with it—at first and when it involves a common gene—a rapid decrease of homozygotes. While the frequency of the gene is decreasing in this way its effect becomes gradually weaker. At low frequencies the effect is without appreciable significance from the point of view of the population. The following is a numerical example. If a gene has the frequency of 0·32 per cent., the character accordingly having the frequency of 1 in 1000, it will take ten generations before it is possible to reduce the frequency of the character-carriers by not quite one-half—that is to say, to 6 in 10,000, provided that all those who have the character are sterilized.

In broad general lines the same issue may be approached from a different point of departure. Suppose a mutation has arisen in the above manner in a population and has gained a certain extension in an isolate. After some time a homozygote arises as the result of in-breeding. By comparison the number of heterozygotes in the isolate will be relatively enormous. So if he is prevented from propagation this does not imply that we appreciably reduce the heterozygotes simultaneously present in the population. The latter reproduce themselves, and therefore the proportion of heterozygotes should be approximately constant, provided that the heterozygotes show the same fertility as the remaining portion of the population. Sterilization or propagation-preventing measures will not be capable of forcing a gene below what I should like to term "the lowest heterozygote frequency."

A good example of a recessive hereditary character which must behave in this manner is juvenile amaurŏtic idiocy. According to Sjögren's investigation, between four and five character-carriers of this type are born in our country annually. In spite of the fact that the homozygotes never propagate the gene has spread to a certain extent, and it is naturally out of the question to force the frequency of the gene down to a lower level by way of propagation-preventing measures, since character-carriers do not reproduce themselves. At the present time we are only in exceptional cases able to recognize the heterozygotes and prevent them from propagation.

In cases of more complicated forms of recessivity we get a similar mechanism. In dihybrid recessivity—that is to say, when two different genes in homozygotic form are indispensable to the development of the character—the figures which correspond to a given frequency of character-carriers depend on the frequency of both the genes in question. If one gene is very common, being present in practically all the individuals in the population, the selected character will behave approximately as if only one gene were involved. For the same frequency of character-carriers this is not so when there is no such disparity. The effect of selection is then essentially weaker than in the case of simple recessivity, and weakest of all when the frequency of the two genes is equal.

When it is a question of simple dominance or those forms of dominance which correspond to complicated forms of recessivity, prevention of propagation or sterility of the character-carriers obviously results in the disappearance of the gene from the population. We may also distinguish a third type of heredity, that is polyhybrid dominance, when at least one gene out of each pair of genes is required for the character to arise. If, to begin with, we take dihybrid dominance, the character should behave approximately as if simple dominance were present, when one of the genes is very common. If, on the other hand, both the genes are equally frequent and the character is rare, what happens recalls the effect of selection on a recessive character of the same frequency. For rare characters it is exceedingly weak. For characters of the same frequency involving more than two dominant genes analogous remarks apply. Other things being equal, selection is weaker when the number of genes is greater and when their individual frequencies are of the same order of magnitude.

2. EFFECT OF INCREASING OR DECREASING CONSANGUINEOUS MARRIAGES.

Such considerations lead us to ask whether we might reduce the frequency of a character in an indirect manner. Homozygotes arise as a result of in-breeding. It is therefore reasonable to expect a reduction of homozygotes if the frequency of in-breeding is lessened. Intermarriage between parental sibs and children of parental sibs occurs only in exceptional cases in human populations. Consequently, the form of intermarriage which is most important is the marriage of first cousins. Intermarriages involving lower grades of consanguinity are sure to be of very little importance individually, and it is not practicable to prohibit them. Hence the effect of preventing first-cousin marriages is most important, and may be dealt with as follows:—

Suppose that a gene which determines a recessive monohybrid character has the frequency r in a given isolate. In amphimixis character-carriers get the frequency r^2. In this situation random intermarriage of first cousins will take place. We may then represent marriages of first cousins by a fraction g, and marriages of a different type, including lower grades of consanguineous unions, by a fraction h, such that $g+h=1$. Among descendants of marriages of first cousins the frequency of recessive character-carriers is $\frac{1}{16}r+\frac{15}{16}r^2$ (*cf.* Dahlberg, 1929). So if p stands for the proportion of recessives in other marriages,

$$r^2=g(\tfrac{1}{16}r+\tfrac{15}{16}r^2)+hp.$$

Solving for p, we obtain

$$p=r^2+\frac{1}{16}\cdot\frac{g}{h}(r^2-r).$$

To evaluate the effect of a reduction in the frequency of marriages between first cousins we assume that we prevent a part, a, of in-breeding of first cousins, counted relative to the whole of the population. Instead of the prevented marriages of first cousins we have to add a corresponding frequency of marriages with the composition represented by p in the above equation. The result is that the population gets the following composition:—

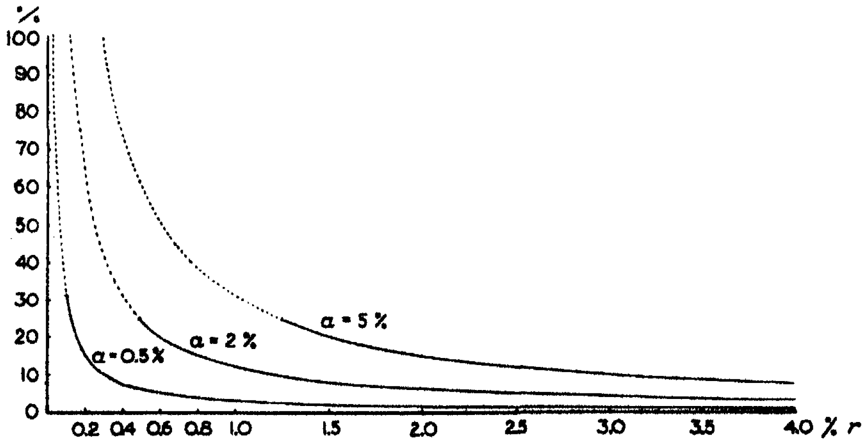
$$r^2+\left\{a\left[r^2+\frac{1}{16}\cdot\frac{g}{h}(r^2-r)\right]+\frac{a}{16}(r+15r^2)\right\},$$

which is equivalent to

$$r^2+\frac{a}{16h}(r^2-r).$$

In order to get an idea of what is meant by this expression we compare it with the composition resulting from amphimixis. The population of recessives is then r^2, so that the decrease is $-\frac{a}{16h}(r^2-r)$; and the ratio of this decrease to the frequency of recessives in amphimixis is $-\frac{a}{16h}\left(1-\frac{1}{r}\right)$.

In this expression h is a number close to 1, since only a very small proportion of marriages occur between first cousins unless the population is very small. When the population is large we can therefore put $h=1$ in order to get a survey of the situation. It should be called to mind that a refers to reduction from frequency of first-cousin unions in amphimixis. From the text-figure we obtain an idea of the effect which is to be expected from an alteration in the frequency of the marriages of first cousins on this assumption. First we assume that $a=0{\cdot}005$, *i.e.* that the proportion of first-cousin marriages prevented is 0·5 per cent. of all marriages. Except when the gene is extremely rare the effect is slight. If the character has a frequency of 4 : 10000, only close on 2 per cent. of the character-carriers will drop out. Only at extremely low frequencies of character-carriers do we get a more noticeable effect. If the gene has the frequency 0·4 per cent., which means that character-carriers at amphimixis have a frequency of 16 : 1000000, 8 per cent. of the character-carriers will disappear. It should finally be pointed out that in case an isolate is so large as to comprise 1000 persons, the lowest conceivable frequency of the gene is 0·1 per cent. There needs must be at least two heterozygotes in the population. Such a frequency of the gene corresponds to a frequency of character-carriers of 1 : 1000000. In this situation we obtain a reduction of the frequency of the character-carriers amounting to 30 per cent., if we prevent 0·5 per cent. of in-breeding, which implies that practically every marriage of first cousins is prevented.



We must bear in mind, however, that this limiting case presupposes not only a very low mutation rate, but also a very small order of sampling error. Where there are only two heterozygotes in isolates, the two heterozygotes in half of them will belong to the same sex. The sex difference gives in this way less weight to the very low frequencies when the frequencies are varying from isolate to isolate. It is obvious that limiting cases with these frequencies must be very rare. It is more reasonable to suppose a somewhat higher frequency of heterozygotes, say at least four heterozygotes in the isolates, as more representative of the limiting case. The largest effect attainable by prohibiting marriages of first cousins is 15 per cent. in that case. Needless to say, this effect is directly attained. No further reduction is subsequently obtainable, and if marriages of first cousins are again permitted with usual frequency we again obtain the original number of character-carriers. An increase or decrease of intermarriage of first cousins carries with it a decrease or increase in the proportion of heterozygotes and a corresponding increase or decrease in the proportion of homozygotes, but does not alter the proportion of genes.

We shall next assume that first-cousin marriages amounting to 2 per cent. of the total population are prevented. It is only when we come to medium-sized or small isolates that it is possible to prevent such a number of first-cousin marriages. In large populations so many marriages between first cousins can hardly be prevented, because they do not generally occur so often. If mating is random this figure is attained in isolates comprising at most one or two hundred persons of full age. Formulæ for the relation between the magnitude of isolates and the frequency of first-cousin unions have been given by Dahlberg (1929). We have employed these formulæ to obtain figures for the instances given here and in the following discussion. In such isolates we cannot obtain extremely low frequencies of character-carriers. When the isolate comprises 200 persons, the lowest conceivable frequency of the gene is 0·5 per cent. With this limiting value we reach the maximal effect if all the marriages of first cousins are removed. Then the frequency of character-carriers decreases by 25 per cent. If we count with four heterozygotes in the isolates, the decrease in the frequency of the character is 12·5 per cent.

If we finally assume that we prevent 5 per cent. of marriages of first cousins, we get down to isolates comprising about 80 individuals. The lowest frequency of character-carriers which is then conceivable is 1·25 per cent. Even in this case the maximal effect will be limited to a disappearance of a little below 25 per cent. of the character-carriers. If, again, we reckon with four heterozygotes in the isolate, the reduction of the character-carriers is only about 12 per cent. We must, however, reckon with the fact that in practice we can hardly expect to prevent all the marriages of first cousins, and that the upper limiting values with which we have counted are only realized under very exceptional circumstances. This being so, measures against marriages of first cousins should hardly be expected to be very effective, and should at best only bring about a decrease in the frequency of rare character-carriers amounting to something like 10 or 15 per cent.

In view of the effect to be expected from an increase in the marriages of first cousins, it should be pointed out that the formula and the figures given above still hold good. But the situation is different in certain respects. Since the frequency of cousin marriages is, however, low in human populations, there is more room for an increase than for a decrease in their frequency. Through an increase of marriages between first cousins rare character-carriers may be more than doubled. This aspect of the matter is only of theoretical interest. Hence we shall not enter further into the problem. It is sufficient to say that the foregoing expression still holds with appropriate change of sign.

The effect of increasing or decreasing the frequency of cousin marriage on the frequency of characters determined by more than one pair of recessive genes is essentially weaker. For dihybrid recessives, when both genes are about equally common, the increase we obtain through marriages of first cousins at a given frequency of character-carriers is essentially lower than the increase obtained at the same frequency of monohybrid recessive character-carriers. For the general case we may argue as follows: When the frequencies are $r_1, r_2, r_3 \dots r_n$, the frequency of the character-carriers is $r_1^2 \cdot r_2^2 \cdot r_3^2 \dots r_n^2$.

Since r is always a number smaller than 1, every r added to such a series means that the frequencies of the earlier terms have to be increased in order to obtain the same product sum as before. An introduction of a fresh term accordingly implies an increase of the earlier frequencies of genes. The portions of the gene frequencies which become manifest under such circumstances are smaller the more numerous are the r's which enter into the series at a certain given frequency of character-carriers. This being so, it should turn out more difficult in one way or the other to affect the frequency of the character so long as the only possibility open to us is to influence the manifest character-carriers. If we want to exterminate them by way of sterilization, the effect consequently is smaller when the character depends on several than when it depends on a single recessive pair. If we wish to affect their frequency by preventing marriages of first cousins, the same argument applies. What applies to multiple recessives applies also to multiple dominants.

In our above analysis we have started from the conception of sharply circumscribed isolates. We have earlier pointed out that this is a schematization of the situation. Actually we seldom meet with distinctly delimited isolates. The probability of a marriage, for instance, decreases with increasing distance. If the distance is large, the probability of a marriage is slight, but in this case the probability of a marriage of first cousins is also slight. If we imagine a person living in an isolate in a valley, we may postulate a given probability that he will marry outside the valley, or, to express it differently, outside the boundaries of the isolate. This probability is very slight. If he does marry outside the isolate, the probability of the person chosen by him being a heterozygote is also slight. Even for a small isolate this corresponds to a low realisable frequency of genes. At the same time the chance of a cousin marriage is slight for such marriages. So if we argue more in agreement with the actual state of things than we have done so far, this should not alter our conclusions.

Published data on the incidence of first-cousin marriages among parents of rare defectives furnish a check on the "lowest heterozygote frequency." For nearly all the clear-cut cases of single recessive autosomal gene substitutions recorded figures are in the neighbourhood of 15 per cent. Thus for juvenile amaurotics Sjögren's data give 15 per cent.; for infantile amaurotics (amaurotic family idiocy) Slome's data give 15 per cent.; for Usher's pedigrees of retinitis pigmentosa 17 per cent.; for Pearson's figures in albinism 17 per cent. The figures for alcaptonuria (between a lower limit of 18 per cent. and an upper of 40 per cent.) and for Friedrich's ataxia (9 per cent.) are based on smaller samples and are subject to a large sampling error consistent with the same view (Hogben, 1931, 1933). We call to mind that the rarer a gene is at monohybrid recessivity the higher is the frequency of first-cousin marriages among parents of character-carriers, and also that we have found the maximal figure attainable at lowest frequency of heterozygotes to lie at about 15 per cent. or somewhat more. This theoretical figure tallies well with the empirical figures. I wish to thank Professor Hogben for having pointed out to me this possibility of checking empirically the theoretical calculation. We may, moreover, infer that whenever incidence of first-cousin marriages among the parents of rare defectives reaches a figure in the neighbourhood of 15 per cent. the gene frequency corresponds to the *lowest* heterozygote frequency as here understood, and that no appreciable effects can be achieved by selection.

3. EFFECT OF INCREASING OR DECREASING SIZE OF ISOLATES.

Another way in which the frequency of rare characters may decrease arises from the circumstance that isolates may grow beyond their original boundaries. If it is a case of a rare character we have to reckon with the isolate receiving an addition from neighbouring isolates from whose population the gene is absent. (In an adjacent isolate a gene corresponding to another defect which may be more or less similar may be present, but it is improbable that it should happen often that the same *rare* mutation arises in *adjacent* isolates.) Through the growth of an isolate in this manner the frequency of the gene decreases, as does also the probability that it will be present in the homozygous state. Simultaneously the frequency of cousin marriages and other consanguineous unions decreases also. Assume that the gene has the frequency r and that the isolate increases by a parts of its original size. The gene frequency will decrease according to the expression

$$\frac{r}{1+a}.$$

This in its turn means that the frequency of character-carriers becomes

$$\frac{r^2}{(1+a)^2}.$$

It appears from this formula that if an isolate increases by 50 per cent., the proportion of homozygotes decreases to 44 per cent. of the original value. If an isolate increases by 100 per cent.—that is to say, if it is doubled—the proportion of homozygotes decreases to 25 per cent. of the original value, 75 per cent. of the homozygote frequency disappearing. It is thus obvious that growth of isolates beyond their boundaries may be expected to have a very important effect on the frequency of rare recessive homozygotes.

If the frequency of character-carriers is reduced in this way on account of the growth of the isolate beyond its boundaries, the lower frequency specified above applies to a larger isolate and to a larger portion of the population. To determine the net gain to the population we must take this fact into consideration. That is to say, the population in which the frequency of recessives is $r^2 : (1+a)^2$ is $1+a$, and the *number* of recessives has therefore decreased to $r^2 : (1+a)$.

In other words, the frequency of recessive character-carriers alters in inverse proportion to the size of the isolate. If the isolate is doubled, the frequency of the recessive characters decreases to one-half of their former frequency.

An alternative analysis of the problem is given in the following:—

Suppose that the composition of a population with respect to a single autosomal gene substitution is represented by *frequencies* $(1-r)^2$DD; $2r(1-r)$RD; r^2RR.

If it consists of a individuals, its *numerical* constitution is

$$a(1-r)^2\text{DD}+2ar(1-r)\text{RD}+ar^2\text{RR},$$

i.e. it contains ar^2 recessives.

Let us now assume that the population is increased to n times its previous size by adding $(n-1)a$ individuals of constitution DD from a neighbouring isolate in which the gene for the recessive condition is absent. Its *numerical* composition is now

$$[(n-1)a+a(1-r)^2]\text{DD}+2ar(1-r)\text{RD}+ar^2\text{RR},$$

and the corresponding *frequencies* of RD and RR in the new population of na individuals are

$$\frac{2r}{n}(1-r)\text{RD};\quad \frac{r^2}{n}\cdot\text{RR}.$$

Recessives are produced from matings RD·RD, RD·RR, RR·RR, which occur at random mating with frequencies

$$\frac{4r^2}{n^2}(1-r)^2;\quad \frac{4r^3}{n^2}(1-r);\quad \frac{r^4}{n^2}.$$

The frequency of RR arising is

$$\frac{r^2}{n^2}(1-r)^2+\frac{2r^3}{n^2}(1-r)+\frac{r^4}{n^2}=\frac{r^2}{n^2}\left\{(1-r)^2+2r(1-r)+r^2\right\}=\frac{r^2}{n^2}.$$

The frequency of RR in the new isolate is therefore $\frac{r^2}{n^2}$ and this (Pearson-Hardy law) is in equilibrium for amphimixis. The number of RR's is therefore $\frac{r^2}{n^2}\cdot na=ar^2/n$.

Hence, when the community increases in numbers from a to na by extension of its boundaries, being multiplied by n, the *number* of rare recessives decreases in one generation from ar^2 to ar^2/n, being divided by n, and remains constant thereafter.

Analogous reasoning applies to a multiple recessive character conditioned by genes with the frequencies $r_1, r_2, r_3 \ldots r_n$. If the isolates increase with a parts of their original size, the frequencies will decrease to

$$r_1/(1+a);\quad r_2/(1+a);\quad \text{etc.}$$

and the frequency of the characters according to the expression

$$\{r_1^2 . r_2^2 . r_3^2 \ldots r_n^2\}/(1+a)^{2n}.$$

As before, the enlargement of the isolate brings with it an increase of heterozygosity at the expense of homozygosity.

It should be called to mind that to the mechanism here under consideration only rare genes and characters are of interest. If a dominant gene has the frequency d, and if the isolates increase by a parts of their former size, the character which originally showed the frequency $2d-d^2$ will now have a frequency

$$2d/(1+a)-d^2/(1+a)^2.$$

If, as before, we take into account the total size of the enlarged isolate, the numerical value corresponding to $2d-d^2$ dominants in the smaller isolates is

$$2d-d^2/(1+a).$$

It thus appears that for a low value of d the increase will be slight. The situation, in point of fact, is this. When the gene is rare, homozygosity is so much less frequent than heterozygosity that a decrease of homozygosity cannot exercise any effect worth mentioning. For rare characters conditioned by a simple dominant gene a growth of the isolate beyond its former boundaries is of little importance. The same is true of more complicated forms of dominance corresponding to complicated forms of recessivity. With multiple dominants we get a different situation. If the character is rare and one gene is very common, what happens approaches what would occur if only one gene were involved. If both of two genes are about equally common, what happens resembles what would occur when a recessive character is involved.

Isolates may therefore grow in two ways. In the first place, an isolate may grow in the way we have above chosen as the starting-point of our last calculation, *i.e.* it may extend its original boundaries. But an isolate may also grow because propagation within the isolate brings with it an increase in its number. The question now is: What does an increase of the latter type signify? If we assume that heterozygotes present in the population are just as fertile as the homozygotes, such an increase of an isolate does not result in any change whatever of the frequency of characters. We get a decrease in the random frequency of in-breeding, but such a decrease in, say, the random marriages of first cousins has no effect at all. When analysing human populations we should bear this state of things in mind.

We have already pointed out that a mutation has a greater chance of spreading in a small than in a large isolate. A growth of the isolates in itself may thus be considered favourable for the reason that new mutations will then not have so powerful an effect as was the case earlier.

In summing up it may thus be pointed out that for reducing rare recessive characters contraceptive measures and sterilizations are of very little importance. Prevention of in-breeding might be conceived of as bringing about a somewhat greater effect. A far more powerful effect, however, may be expected when isolates grow beyond their boundaries. Growth of the isolates owing to increase of population within the isolates, on the other hand, is of no importance. We disregard the possibility that isolates showing rare genes of defects grow more than other isolates, or reversely.

4. ACTUAL SIZE OF ISOLATES.

In the light of the foregoing treatment it may be of interest to try to arrive at a conception of the manner in which isolates behave in the European countries. The frequency of in-breeding provides an indicator of the size of the isolates. Official data regarding in-breeding are given by France, Bavaria, and Prussia for prolonged periods of time. We shall now discuss some figures obtained from the official statistics of these countries.

In the first place, we must remember that an increase in population has taken place in these countries. If the different types of isolate showed proportional increase, increase of total population might appear to be a gauge of the growth of the isolates in so far as it is conditioned by the increase in population. In reality the situation is not as simple as that. Alongside of the increase in population a removal to the towns has taken place. This implies that increase in population has, above all, meant an increase of isolates of the towns. At the same time, however, owing to the development of communications, isolation boundaries have been broken up in the rural districts. This would make for larger rural isolates. To a certain extent the isolates have accordingly grown within themselves, the frequency of in-breedings on this account decreasing. Simultaneously to a very great degree isolates have also grown beyond their boundaries. Figures for Prussia are given in Table I. The table shows that marriages of first cousins have decreased from 0·71 down to 0·20 per cent. in the fifty years between 1875 and 1926. Marriages between parental sibs and children of parental sibs have decreased in about the same proportion. At the present time the frequency of in-breeding is barely one-third of what it was fifty years ago. Simultaneously the number of contracted marriages has increased almost to double. By itself this increase would promote a decrease of in-breeding which is of no importance to the frequency of rare recessive character-carriers. If the increase in population had resulted in a quite indifferent increase in the isolate, marriages of first cousins would have decreased to about 0·40 per cent. The actual decrease to 0·20 per cent. would imply that the isolates had also grown beyond their boundaries, so that on an average they had been approximately doubled. Without being able to give an exact figure, we are thus justified in stating that the isolates have grown beyond their boundaries to the effect that they have increased by essentially more than 100 per cent. This applies to the average isolate. The increase, no doubt, would be greater for the isolates of the towns than for those of the country districts.

TABLE I.—PRUSSIA.

Period of Time.	Number of Contracted Marriages.	Out of which (%) Marriages between	
		Cousins.	Uncle-niece or Aunt-nephew.
1875–1880	1286339	0·71	0·08
1881–1885	1104219	0·68	0·07
1886–1890	1180661	0·58	0·06
1891–1895	1244390	0·51	0·05
1896–1900	1400381	0·44	0·04
1901–1905	1450203	0·42	0·03
1906–1910	1552411	0·42	0·03
1911–1915	1436963	0·35	0·03
1916–1920	1678775	0·32	0·03
1921–1926	2122300	0·20	0·03

In Table II figures from Bavaria for the corresponding period of time are given. We here find a somewhat more marked displacement. The frequency of in-breeding seems to have decreased to less than one-quarter, and in the case of Bavaria it is also probably true that isolates have grown beyond their boundaries considerably more than 100 per cent. Table III gives figures from France. Curiously enough, we find here a fairly constant frequency of cousin marriages of about 1 per cent., together with an approximately constant number of contracted marriages. The number of contracted marriages naturally is not an altogether exact measurement of the growth in population, which is important to our problems. Neither is total number of population a correct measurement. A more suitable measurement is the number of individuals in the ages in which the marriage is contracted. An exact analysis of the problem not being possible, we have in the tables been content with figures showing the number of contracted marriages as an approximate indicator of the growth of the population.

TABLE II.—BAVARIA.

Period of Time.	Number of Contracted Marriages.	Out of which (%) Marriages between	
		Cousins.	Uncle-niece or Aunt-nephew.
1876–1880	188973	0·87	0·10
1881–1885	182553	0·75	0·12
1886–1890	192088	0·60	0·07
1891–1895	210584	0·48	0·05
1896–1900	241571	0·46	0·04
1901–1905	242606	0·42	0·05
1906–1910	250672	0·40	0·05
1911–1915	215291	0·35	0·06
1916–1920	303709	0·38	0·05
1921–1925	305956	0·31	0·06
1926–1933	474268	0·20	0·04

TABLE III.—FRANCE.

Period of Time.	Number of Contracted Marriages.	Out of which (%) Marriages between	
		Cousins.	Uncle-niece or Aunt-nephew.
1876–1880	1410889	1·03	0·08
1881–1885	1420383	1·02	0·07
1886–1889	1110050	0·98	0·09
1891–1895	1142329	0·86	0·06
1896–1900	1463648	0·90	0·05
1901–1905	1495595	0·87	0·05
1906–1913	2470586	1·02	0·04
1914–1919	1350683	0·97	0·03

In order to be able to analyse the situation more closely we give in Table IV figures from Bavaria and Prussia with division into town and country, and in Table V figures from France with division into the department of Seine, and the towns and country in the rest of France. First, as regards Prussia, we find for the towns a decrease of in-breeding by about one-third, a decrease which approximately corresponds to the increase in the number of contracted marriages. This latter increase is essentially conditioned by immigration, so it is the true expression of the isolates having grown beyond their boundaries. As regards the rural districts, we find a decrease of cousin marriages to not quite one-half,

TABLE IV.

Period of Time.	Number of Contracted Marriages.		Out of which (%) Marriages between			
			Cousins.		Uncle-niece or Aunt-nephew.	
	Towns.	Country Districts.	Towns.	Country Districts.	Towns.	Country Districts.
			France.*			
1898–1905	999080	1378527	0·61	1·07	0·05	0·05
1906–1910	699704	851882	0·61	1·39	0·04	0·05
			Bavaria.			
1892–1895	48145	121039	0·17	0·60	0·02	0·07
1896–1900	79414	162157	0·17	0·61	0·02	0·06
1901–1907	98507	245091	0·15	0·52	0·03	0·06
			Prussia.**			
1875–1880	492624	793715	0·58	0·92		
1886–1890	509111	671550	0·50	0·74		
1891–1895	552794	691596	0·46	0·64		
1896–1900	653581	746800	0·40	0·54		
1901–1905	700131	750072	0·39	0·52		

* The figures for dep. Seine (Paris and its environment) are included in towns.
** The table accounts for all consanguineous marriages.

TABLE V.—FRANCE.

Period of Time.	Number of Contracted Marriages.			Out of which (°/o) Marriages between					
				Cousins.			Uncle-niece or Aunt-nephew.		
	Seine.	Towns.	Country Districts.	Seine.	Towns.	Country Districts.	Seine.	Towns.	Country Districts.
1898–1905	271054	728029	1378527	0·96	0·48	1·07	0·09	0·04	0·05
1906–1910	203444	496260	851882	0·64	0·60	1·39	0·05	0·03	0·05

the number of marriages having somewhat decreased at the same time. This points to the isolates in the country districts having almost doubled beyond their former boundaries. In view of the fact that the increase in population above all refers to the towns and with regard to the figures in Table IV, there is reason to suppose that the increase in population to a very small extent is referable to a growth within the isolates, but has practically completely meant a removal of the population from the country into the towns. At the same time the isolate boundaries have been broken up in the country, the isolates here being practically doubled. We have a strong support for our statement that the isolates have increased by more than 100 per cent. in the case of Prussia. Perhaps 200 per cent. would be nearer the mark.

If we now look at the figures from Bavaria, we find a still more marked difference in the frequency of in-breeding between town and country than in Prussia. We also get a decrease in the frequency of in-breeding for the period of time embraced by the figures, which is comparatively short (1892–1907).

If finally we turn to the figures from France we get a marked decrease for the department of Seine, which includes Paris, and rather an increase in the other towns and in the country. It is of further interest to note that the population of Seine has increased considerably, whereas towns and country for the period of time under consideration show a fairly constant annual number of contracted marriages. A more exact conception of the situation is difficult to obtain as figures for a prolonged period of time are lacking. It should, however, be remembered that according to official statistics that part of the population in France which lives in the country has showed both an absolute and percentage decrease during the last fifty years. In 1871 the rural population made up 69 per cent. of the total population, and in 1926 51 per cent., in spite of the incorporation of Alsace-Lorraine. We must further reckon with the fact that the absolute number of individuals in the rural districts has decreased, during the years 1871–1911, from 24·9 millions to 22·1 millions—that is to say, it has decreased by more than 10 per cent. We have thus reason to suspect that the mechanism in France is this: the isolates have decreased in the country districts through removals to the towns—above all, to the big towns. The population in France has kept comparatively constant, and it is here chiefly a case of an interior removal which should result in a decrease of in-breeding in towns and possibly an increase of in-breeding in the country, so that with regard to the country at large the frequency of in-breeding has kept fairly constant.

We should also take into account the extent of immigration into France. It might also be well to remember that in France the parental influence on the contracting of marriage is considered to be much greater than in other countries. In view of this fact, and as we lack figures on which a more exact analysis of the situation could be based, it will hardly be possible to arrive at more definite conclusions as to the situation in this country.

What we can say is that a redistribution of population, such as to decrease isolates in the country districts and to increase them in the towns, in the long run ought to result in reducing the frequency of rare recessive defects. Emigration resulting in a lessening of the small isolates in the country districts will not generally be selective with regard to heterozygotes, and consequently ought not to alter the proportion of genes of the small isolates. A decrease in the frequency of in-breeding as well as an increase of this frequency does not necessarily in all circumstances affect the frequency of character-carriers in an isolate. If, as a consequence of emigration, the frequency of in-breeding increases in the rural districts, this does not result in an increase of the homozygotes. As the rural isolate now becomes smaller, the process means a gain from the point of view of the population in spite of the fact that the frequency of character-carriers in the rural isolate itself keeps constant. At the same time emigration brings about an increase of the town isolate, and this in its turn results in a lowered frequency of genes and a decrease of homozygotes, which to the population means a further gain.

In summing up it should also be pointed out that, when recessive defects are rare, noteworthy effects can hardly be attained through sterilization or contraceptive measures. By lowering the frequency of marriages of first cousins a somewhat larger, although even at best only moderate, decrease of homozygotes may be obtained. In European countries the development of communications and industrialization has resulted in a growth of isolates, such as is sure to be of very great significance. Processes of this type may be expected to be vastly important. For France we have not been able to arrive at figures which make possible a definite estimate of the situation. For Prussia and Bavaria we have been able to show that isolates have been more than doubled on an average, which means that rare recessive characters have decreased by at least one-half. Under such circumstances we have reason to believe that the exhibition of certain hereditary defects is at the present time decreasing in frequency. With regard to such characters, attempts to keep the population in the rural districts must be looked upon as less suitable from a eugenic point of view. If, when speaking of the *degeneration* of civilized peoples, we refer particularly to rare recessive defects, there is no reason to suppose that such a degeneration is just now taking place. We might more properly speak of a *regeneration*.

Finally, it should be emphasized that we must not apply the analysis presented above too rigidly. We want a more detailed knowledge of population processes going on at the present time. We also want a more detailed insight into hereditary characters which are of interest in this connection. In order to give a more concrete touch to this reservation we should recall that in a number of countries, above all in Sweden, it has been possible to show that stature has increased considerably in modern times. In Sweden stature has increased about 1 dm. in 100 years. Hultkrantz (1927) points out considerations which militate against the belief that this increase is exclusively conditioned by a higher standard of living. The increase may also be conditioned by breaking up isolate boundaries which in the course of several generations may result in displacements towards increased heterozygosity for accumulative multiple genes. It is also conceivable that extremely high intelligence is conditioned by a number of genes, and that we have here a similar mechanism. If growth of isolates has brought about an increase in average stature and in the number of persons who are extremely tall, it might also bring about an increase in genetically determined average intelligence and in the number of extremely intelligent individuals. These questions, of course, are of vital importance. Whatever happens, there is no possibility to reverse the process. To return to the defectives, it is naturally also possible that certain hereditarily conditioned defects may behave in the same manner and that we have obtained an increase of certain deficient types through breaking up of isolates.

The rural exodus is a highly debated question nowadays. In the above discussion we have tried to analyse certain aspects of this problem and have made an attempt to arrive at more definite conclusions on certain points, but we have by no means been able to treat the problem in full.

5. SUMMARY.

It is well recognized that complete selection has a very slight effect on the frequency of rare defects determined by one or more recessive or by several dominant genes. The present communication discusses other ways in which the *exhibition* of rare defects of this type may be reduced numerically. Consanguineous marriages may increase or decrease in two ways. Thus the number of chance unions of this kind in a system of random mating depends on the size of the population *isolate*. Increasing them by diminishing, or decreasing them by extending, the size of the *isolate* has no effect. The effect of preventing consanguineous unions which would otherwise occur by chance depends on the rarity of the gene, and this is limited by the size of the isolate. Analysis

shows that preventing all consanguineous unions has relatively little effect on the incidence of rare defects owing to the existence of this limit. Contrariwise, the effect of enlarging the size of an isolate, as by extending communications or removing social taboos, is to produce a proportionately large reduction in the incidence of rare defects. The significance of this fact as bearing on social policy and recent population movements is discussed.

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ADDENDUM.

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Figures from Italy obtained after the above was sent in for publication show a decrease in the frequency of first-cousin marriages from 0·77 per cent., 1868–70, to 0·44 per cent., 1931–35. We have the same trend in regard to in-breeding in Italy as in Prussia and Bavaria, and the same conclusions may consequently be drawn for Italy as for Germany.

(*Issued separately September* 30, 1938.)

XVI.—Two Cases of Malformation of the Gill-covers in Salmon.

By **Dr V. Tchernavin**, Department of Zoology, University of Edinburgh. *Communicated by* Professor JAMES RITCHIE, M.A., D.Sc. (With One Plate and Two Text-figures.)

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ONLY a small number of salmon smolts (*Salmo salar*) that leave the river for the sea return for spawning (Calderwood, 1930, p. 180; 1931, pp. 36, 56; Menzies, 1931, p. 60; and others). The large loss of adolescent fish seriously affects the stock of salmon in the rivers, so that the question of possible causes of the death of salmon in the sea is one of some practical interest.

Direct observation of salmon in the sea is very difficult, and very little is known about a salmon during this important period of its life. Thus there is a wide field for conjecture about the conditions of life for salmon during that period, and about the causes of the large mortality. It would be simple to suppose that during the sojourn in the sea the salmon compete in a fierce struggle for existence, and that the survivors represent the fittest individuals.

Such reasoning would seem logical but for the fact that among salmon (also sea-trout and the Pacific migratory salmon) entering the rivers there is always a considerable number of malformed specimens which could by no means be considered the fittest. Their abnormalities are sometimes so great as to make it difficult to understand how they could survive, because such specimens would appear to be the first to succumb in any struggle for existence. The pug-headed specimens which have been recorded among different Salmonidæ (Stoddart, 1836; Cuvier and Valenciennes, 1848; Coolidge, 1870; Carlet, 1873; Young, 1901; Hofer, 1904; Grote, 1909; Malloch, 1910; Soldatov, 1912; Gemmill, 1912; and others) obviously could not be good fighters and must have great difficulty in taking food, for Cuvier and Valenciennes showed long ago (1848, pp. 334–335) that in these monsters the upper jaw is bent in such a way that the teeth of the premaxillary meet those of the palatine. However, malformed salmon enter fresh water in good condition as regards nourishment, and spawn. This fact suggests that during their sojourn in the sea there was a superabundance of food, available even for pug-headed individuals which could only use the lower jaw in obtaining nourishment.

More frequent still are deformations of the body where the vertebral column is curved or the vertebræ fused, or where large portions of the muscles of the body are defective and contracted, as has been described by Barrington, 1747, 1768; Hofer, 1904; Ritchie, 1908; Grote, 1909; Malloch, 1910; Gemmill, 1912. Salmon with more or less deformed muscles are found in hundreds in every river entered by salmon in large numbers. These specimens cannot be perfect swimmers, and we may conclude that they could survive only because during their sojourn in the sea they found enough room to be free from the pursuit of enemies, and could obtain food without difficulty or competition.

Quite frequent also in salmon are cases of deformities and malformations that seem to be of minor significance and do not attract much attention. Nevertheless, investigation shows that such cases may involve grave deterioration of the general condition of the fish. Such are, for instance, the frequent malformations of the gill-covers in salmon and trout. Two examples of deformity of the gill-covers are described below.

A study of malformed specimens of salmon, obviously inferior physically, which nevertheless ascend the rivers with the normal and healthy fish, suggests that during the sojourn of the salmon in the sea there is no real struggle for existence, or competition where the strongest and fittest survive. It seems more probable that the heavy loss of life is due to periodical catastrophes, or to the invasion of enemies, greatly surpassing the salmon in size and speed, which destroy large numbers of salmon without special regard to their fitness.

We may suppose that these disastrous periods of salmon life are of short duration, and are succeeded by long periods when the individuals have time for their wounds to heal and the salmon enjoy comparative freedom from attack and abundant food.

DESCRIPTION OF MALFORMATION OF THE GILL-COVERS IN SALMON.

In Salmonidæ the branchial cavities are very large, and the gill-covers forming their outer walls are of great importance. They play an essential rôle in the respiratory and feeding processes, and protect the tender gills from outside injuries and the intrusion of parasites. In accordance with the significance of the gill-covers their structure is of great perfection. They have a well-developed skeletal basis and an elaborate system of muscles and ligaments which make possible the rhythmic movements of the opercula and a perfect closing of the branchial apertures. The skeleton of the gill-covers consists on either side of fourteen or fifteen well-developed bones; three of them have the form of large plates covering the cavity laterally, and a series of eleven or twelve narrow and sabre-shaped bones securely protect the cavity on the ventral side. In spite of the importance of the gill-covers, many salmon and trout return to the rivers having their gill-covers gravely deformed and functioning only partially.

Last autumn I studied fifteen specimens of salmon in breeding condition from the Rivers Don and Dee in Aberdeenshire, Scotland. Among them there were three with markedly deformed gill-covers on one side, one of which is shown in text-fig. 1. Recently I received for investigation yet another specimen from the same district in which both gill-covers were deformed (text-fig. 2).

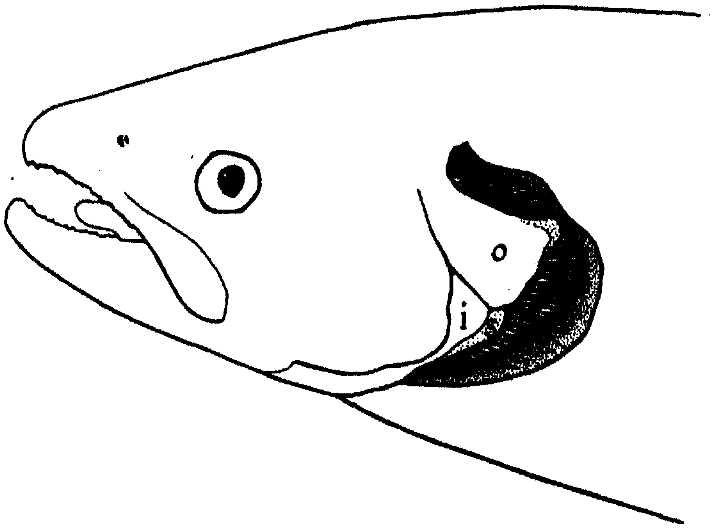

Fig. 1.—Head of *Salmo salar* with deformed gill-cover. Female, no. 4 S; ripe.
Left side. Diagrammatic.
i = interoperculum; *o* = operculum; *s* = branchiostegal ray.

Case 1.—*Salmo salar*, no. 4 S, female, breeding; River Don, Aberdeenshire, 4.11.37. Length 602 mm. (text-fig. 1 and Pl., fig. 1).

The left gill-cover is deformed and only partially covers the branchial cavity (text-fig. 1). The greater part of the gills on this side is exposed laterally and ventrally. Examination showed that the malformation was due to some damage received a long time previously, very likely before the fish went out to sea. The damage was completely healed.

Dissection revealed that the greater part of the opercular bone was bent inwards and was growing inside the branchial cavity. Only part of it could protect the gills. The subopercular was reduced to the size of a large scale. Only four branchiostegal rays were present, of which the two first were greatly reduced in size and the two hinder ones were noticeably deformed. The ventral part of the epihyal was cut off, and the cartilage surrounding the posterior end and the ventral edge of the epihyal absent. The effects correlated with this deformity were as follows. The preopercular grew much stronger and broader, especially its horizontal lobe; also much enlarged and stronger was the interopercular; the hyoid bar was somewhat lengthened, and the whole left side of the skull seemed to be less developed than the right. That was especially clear in the case of the parasphenoid and supraethmoid, both having the left sides noticeably less developed than the right ones. The gill-arches of the left side were shorter than those of the right; the number of gill-rakers less numerous. Finally, and this is perhaps the most vital consequence, the gill-filaments of the left side were greatly reduced in size (Pl., fig. 1).

The results of this investigation are shown quantitatively in the following tables, all measurements being recorded in millimetres:—

TABLE I.—BONES OF THE GILL-COVERS AND THE HYOID BAR.

Name of Bones.		Right (normal). mm.	Left (malformed). mm.
Opercular—	length	39·0	33·0
	breadth	40·0	20·0
Subopercular—	length	37·0	11·0
	breadth	17·0	12·0
Interopercular—	length	30·0	40·0
	breadth	20·0	17·0
Preopercular—	length	45·5	45·5
	breadth	17·0	20·0
Branchiostegals—	1st	20·0	6·5
	2nd	22·0	6·0
	3rd–9th	normal	absent
	10th	34·0	30·0
	11th	38·0	33·0
Hyoid bar—	length	19·5	21·0
	breadth	20·0	17·0

TABLE II.—MEASUREMENTS OF THE GILL-ARCHES (WHOLE LENGTH).

	Right (normal). mm.	Left (malformed). mm.
1st arch	80·0	75·0
2nd ,,	74·5	71·5
3rd ,,	65·0	61·0
4th ,,	59·0	56·0
5th ,,	28·0	26·0

TABLE III.—NUMBER OF GILL-RAKERS.

	Right (normal).	Left (malformed).
Total for the outer rows .	81	76
Total for the inner rows .	43	38
Total . .	124	114

TABLE IV.—LENGTH OF LONGER GILL-FILAMENTS OF THE OUTER ROW IN THE CERATOBRANCHIALS.

	Right (normal).	Left (malformed).
	mm.	mm.
1st arch	25·0	13·0
2nd ,,	22·5	17·5
3rd ,,	22·0	17·5
4th ,,	21·0	18·0

Case. 2.—*Salmo salar*, no. 18 S, male; River Don, Aberdeenshire, 18.1.38. Length 800 mm.; according to information from the Bacteriology Department of Edinburgh University, from which this head was received for investigation, the fish had partially spawned. Breeding characters moderately developed; scales silvery, no red spots; muscles intensely pink; the hook in the lower jaw very small; breeding teeth moderate; gill-covers on both sides deformed; the deformation on the right side was much more marked than that on the left (text-fig. 2 and Pl., fig. 2).

Deformation on the Right Side.

At first sight it seemed that the gill-cover (with all branchiostegals) was almost entirely absent, the gills being entirely exposed laterally and ventrally (text-fig. 2). But closer investigation showed that the operculum and the branchiostegals were sharply bent inwards, embraced the hyoid arch and formed inside the branchial cavity a large pocket open towards the mouth aperture. The inner wall of this pocket was formed by the gill-cover, whose normal function is to enable the gills to be bathed with water entering through the mouth, but which in this specimen closed the branchial cavity from inside and separated it from the mouth cavity. The other function of the normal gill-cover is to protect the gills from outside. In this specimen the gill-cover does not protect them at all, but strongly presses on the first gill-arch, with the result that the gill-filaments are turned with their hinder ends outwards and stick out of the branchial cavity. Examination of the bones of the operculum showed that the opercular was bent back in such a way that only a small upper part of it, 8 mm. long, where the opercular articulates with the hyomandibular, grew in the normal direction (backwards from the hyomandibular and outside the branchial cavity). All the rest, having a length of 40 mm., had grown in a direction opposite to the normal, *i.e.* forward and inside the branchial cavity. Such also was the case with the subopercular, which at the same time was set much lower than normal, and with the interopercular, both these bones being bent back and growing in the direction opposite to the normal. All the branchiostegals were abruptly bent at their bases round the hyal bar and directed inside the branchial cavity. The branchial arches, pressed laterally by the deformed gill-cover, occupied only half the room in the branchial cavity that they would occupy normally. All the arches were thin and weak. The first ceratohyal, which normally is straight, in this specimen was markedly curved. The gill-rakers were malformed, had various shapes and were variously directed, those of the first arch being immovable and closely pressed to the arch. The gill-filaments were abnormally short, curved and directed without any order. The gills were largely infected with "gill maggots" (*Lernaeopoda salmonea*). The second "copula" (posterior basibranchial) had moved towards the right side.

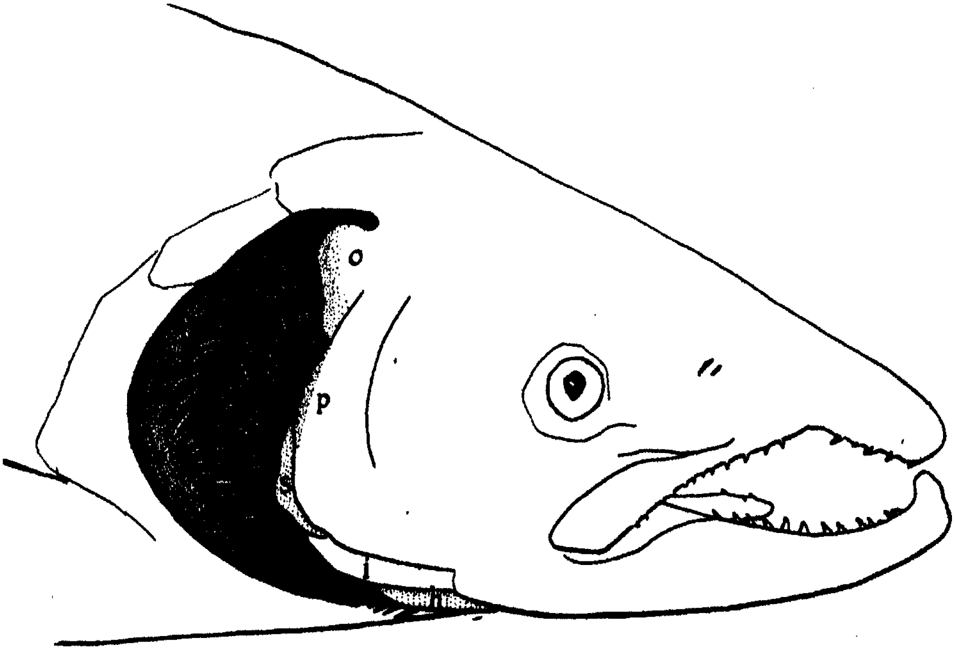

FIG. 2.—Head of *Salmo salar* with deformed gill-cover. Male, no. 18 S; ripe. Right side. Diagrammatic.
i = interoperculum; *o* = operculum; *p* = preoperculum; *h* = hyoid bar; *s* = suboperculum.

Deformation on the Left Side.

The left gill-cover was deformed, but in less degree than that of the right side. The greater part of the opercular was sharply doubled backwards. The subopercular was reduced in size and of irregular shape. Consequently only half of the branchial cavity was covered by the operculum, the hinder part of the gills being unprotected laterally. The interopercular and the branchiostegals were normal, and protected the branchial cavity from beneath. The upper gill-rakers on the epi- and glosso-hyals of the outer row in the first arch were pressed closely to the arch and were immovable.

Effects of the Deformities of the Respiratory Apparatus upon the Chondrocranium (Pl., fig. 2).

There was no trace of any outside injury on the head of this specimen except the deformation of the gill-covers. The chondrocranium itself had also no marks of injuries or fractures. The chondrocranium, however, was markedly abnormal. Its length surpassed the maximum breadth less than twice, *i.e.* was noticeably shorter than that of a normal fish of the same size, sex, and stage of sexual development. The right side of the chondrocranium was less developed than the left one. The right side of the cranial case, the right orbital groove, and the right half of the ethmoid portion were noticeably shorter than the left ones, and consequently the whole chondrocranium was curved towards the right.

These malformations in the chondrocranium may be regarded as the effect of the abortive development of the right half of the respiratory apparatus due to the strong deformity of the right gill-cover.

The two cases of deformation of the gill-covers described above show:

1. That malformations which could be considered as superficial and of minor significance can deeply affect the organisation of the fish.

2. That even such gravely weakened specimens, with conditions obviously inferior to the normal, yet succeed in escaping from enemies and finding sufficient quantities of food during their sojourn in the sea.

The malformations described in *Salmo salar*, no. 18 S, are shown quantitatively in the following table:—

[TABLE

TABLE V.—THE EFFECTS OF THE STRONG DEFORMITY OF THE RIGHT GILL-COVER UPON THE GILL-ARCHES, GILL-FILAMENTS, AND THE CHONDROCRANIUM.

1. *Gill-arches:*

	Right.		Left.	
	Length.	Breadth.	Length.	Breadth.
	mm.	mm.	mm.	mm.
1st	101·5	4·0	106·0	8·5
2nd	91·5	4·5	94·0	7·5
3rd	86·5	6·0	88·0	8·0
4th	62·0	6·0	62·5	8·0
5th	32·0	4·0	32·0	4·5

2. *Length of the Gill-filaments on the Ceratobranchials:*

	Right.	Left.
	mm.	mm.
1st	12·5	30·0
2nd	22·0	31·0
3rd	20·5	32·5
4th	20·5	31·5

3. *Chondrocranium:*

	Right.	Left.
	mm.	mm.
Whole length	115·5	119·5
Length of cranial case	39·0	41·0
Length of orbital groove	29·5	32·0
Length of ethmoidal portion	48·5	50·0

SUMMARY.

Deformities of the gill-covers in salmon may affect the whole gill apparatus, and even the chondrocranium and the bones related to it. Specimens are described with malformed gill-covers, where the gill-arches were shorter than normal, the gill-filaments greatly reduced in size, the gill-rakers reduced in number and degree of development. In a specimen where the right gill-cover was greatly deformed, the whole right side of the chondrocranium was distinctly reduced in size, as also were the parasphenoid and supraethmoid bones.

Nevertheless such specimens, essentially weakened by their deformities, reach the rivers in a good state of nutrition. This fact would suggest that the well-known phenomenon of heavy loss of life of salmon in the sea is probably due to periodical catastrophes of short duration, succeeded by long periods when the individuals have time to heal their wounds and enjoy abundant food.

The work of this paper was done in the Department of Zoology of Edinburgh University, and I should like to thank warmly Professor James Ritchie for his kindness in granting me all facilities, for his helpful advice,

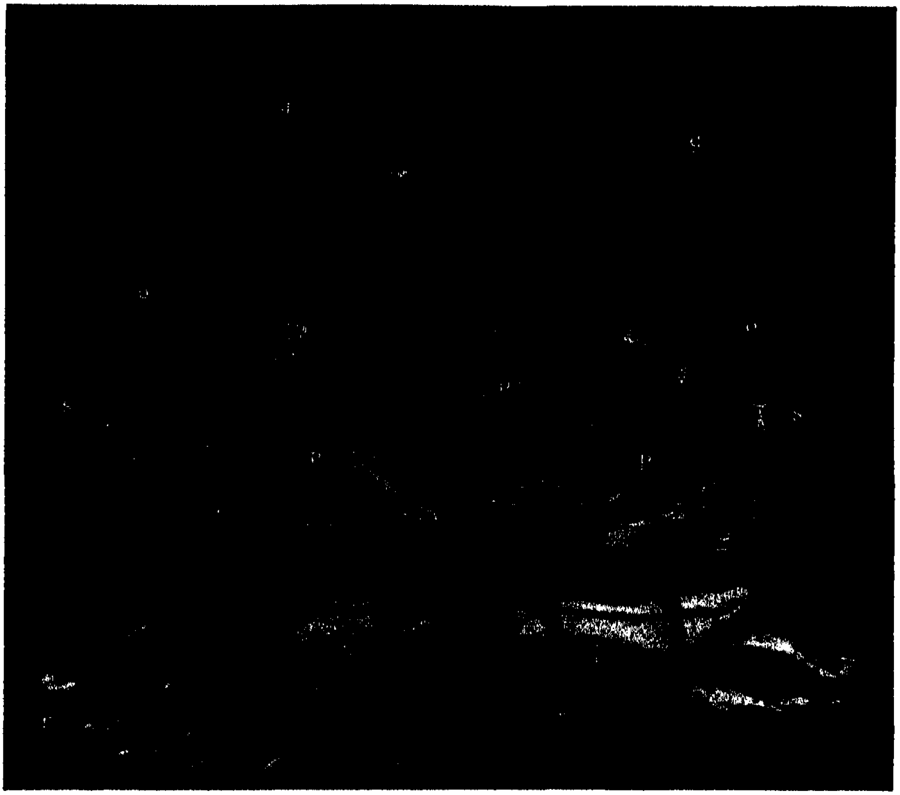

Fig. 1.

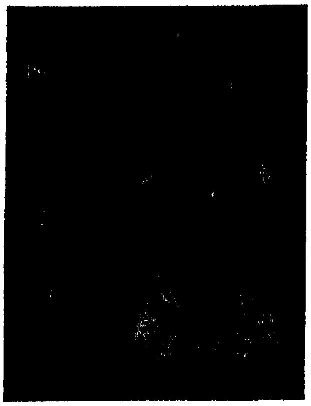

Fig. 2.

V. Tchernavin.

and for reading my paper in manuscript. I am also greatly indebted to Mr W. J. M. Menzies of the Fishery Board for Scotland, who kindly provided me with the necessary material. I must also thank Mr R. J. Fant for preparing the two photographs.

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DESCRIPTION OF PLATE.

FIG. 1.—Elements of the respiratory apparatus of *Salmo salar*. No. 4 S. Left side deformed.

g = 1st gill-arch; *h* = hyoid bar; *i* = interopercular; *o* = opercular; *p* = preopercular; *pa* = parasphenoid; *r* = radii branchiostegi; *s* = subopercular.

FIG. 2.—Chondrocranium and parasphenoid (*pa*) of *Salmo salar*, no. 18 S. Ventral view. The right side is less developed than the left one—the effect of the strong deformity of the right gill-cover.

(*Issued separately November* 11, 1938.)

XVII.—The Dynamics of Sheet Intrusion. By E. M. Anderson, M.A., D.Sc., F.G.S. (With Three Text-figures.)

(MS. received April 25, 1938. Revised MS. received September 29, 1938. Read June 6, 1938.)

THIS communication is largely founded on a paper entitled "Stresses in a Plate due to the presence of Cracks and Sharp Corners," delivered by Professor C. E. Inglis, to the Institution of Naval Architects (1913). The importance of this contribution to the theory of fracture is recognized, and the results seem, among other things, to have a bearing on some geological problems. They may help, for instance, to explain the inception and development of sheet intrusions, under which class one may include ordinary vertical dykes (but not ring-dykes), horizontal sills, and other hypabyssal bodies whose thickness bears only a very small proportion to their length.

SHEET INTRUSION.

Professor Inglis deals with the cases of an infinite solid in the condition of "plane strain," and of an uniform lamina under "plane stress," but it is the former case only which here concerns us. He supposes that there are cylindrical cavities in the materials, with generators which are normal to the plane. The cross-section of any cavity is an ellipse, but in the limit the ellipse may contract into a line of definite length, and the cavity into a plane crack. The results are obtained by the use of elliptic co-ordinates. These are connected with the cartesian co-ordinates x and y by the relations

$$x = c \cosh \alpha \cos \beta,$$
$$y = c \sinh \alpha \sin \beta.$$

The x direction is that of the major, and the y direction of the minor axis of any ellipse, while c is the distance of either focus from the centre, which is the origin. The boundary of any cavity is given by making α equal to some quantity α_0. For the limiting case of the crack, $\alpha_0 = 0$, and $2c$ is then the length of the line, or the extension of the crack in the plane of the co-ordinates. Formulæ are given for the displacements and stresses surrounding any such crack or cavity, when the material is subjected to any system of stress which is uniform at infinity. These satisfy the equations of equilibrium, and in each case also the appropriate boundary conditions.

One may consider first the case of a tension, which becomes equal to

R, and is the same in all directions, at an infinite distance from the cavity. The displacements may be denoted by u_α and u_β, in the two orthogonal directions corresponding at any point to an increase of α and of β. In the same way the stresses at any point may be defined by the three quantities $P_{\alpha\alpha}$, $P_{\alpha\beta}$ and $P_{\beta\beta}$. For the case of the crack, Inglis's results lead to the expressions

$$\left.\begin{aligned}
P_{\alpha\alpha} &= R\frac{\sinh 2\alpha(\cosh 2\alpha - 1)}{B^2} \\
P_{\alpha\beta} &= R\frac{\sin 2\beta(\cosh 2\alpha - 1)}{B^2} \\
P_{\beta\beta} &= R\frac{\sinh 2\alpha(\cosh 2\alpha - 2\cos 2\beta + 1)}{B^2} \\
\frac{u_\alpha}{h} &= \frac{c^2R}{4\mu}[(1-2\sigma)\cosh 2\alpha - 2(1-\sigma)\cos 2\beta + 1] = Ru_1, \quad \text{say} \\
\frac{u_\beta}{h} &= 0
\end{aligned}\right\}, \qquad (1)$$

where $B = (\cosh 2\alpha - \cos 2\beta)$, and $h^2 = \frac{2}{c^2B}$, while σ is Poisson's ratio, and μ the modulus of rigidity. It will be seen that the tractions all vanish where $\alpha = 0$, that is along the margins of the crack. An exception to this occurs where $B = 0$, that is at the extremities. This point will be returned to later.

As u_β is zero, the displacements at all points are tangential to the hyperbolæ which have the extremities of the crack as foci. As one is dealing with a two-dimensional problem, the principal directions of stress can be indicated by the construction of isostatic surfaces. The angles θ formed by these with the directions of the hyperbolæ are given in general by

$$\tan 2\theta = \frac{2P_{\alpha\beta}}{P_{\alpha\alpha} - P_{\beta\beta}}.$$

The principal tensions or pressures (pp) are determined in every case by the formula

$$(pp) = \frac{P_{\alpha\alpha} + P_{\beta\beta}}{2} \mp \tfrac{1}{2}\sqrt{(P_{\alpha\alpha} - P_{\beta\beta})^2 + 4P_{\alpha\beta}^2},$$

the negative sign being taken for the principal stress at any point across that isostatic surface along which $\frac{d\beta}{d\alpha}$ is of the same sign as $P_{\alpha\beta}$. We have also

$$\tan(x, v) = \tan\beta/\tanh\alpha, \quad . \quad . \quad . \quad . \quad . \qquad (2)$$

where (x, v) is the angle made by the hyperbolæ with the axis of x. From (1) and (2) it is easily shown that

$$\tan 2\theta = -\frac{\tanh\alpha}{\tan\beta} = \tan\left[(x, v) \pm \frac{\pi}{2}\right].$$

Hence if ϕ be the angle made by an isostatic surface with the direction of the crack

$$\phi = \theta + (x, v) = \tfrac{1}{2}(x, v) \pm \frac{\pi}{4}.$$

The surfaces may be traced by using this formula, and are the same as those of the related dynamical system which is illustrated in fig. 1.

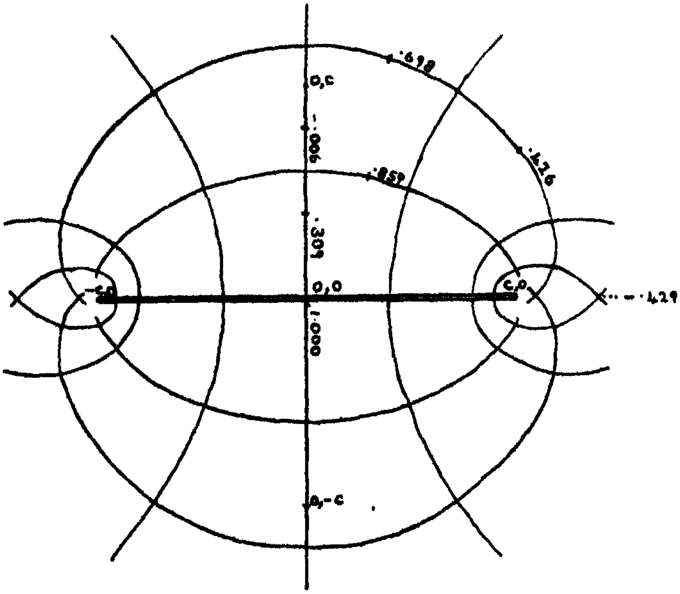

FIG. 1.—Isostatic surfaces. Intrusion into solid not previously under stress. Figures show transverse pressures, as fractions of pressure of magma.

Another case investigated assumes the tension at infinity to be uniform in the direction perpendicular to the crack, there being neither tension nor pressure in the parallel direction. Denoting the tension as before by R, Inglis's data now lead to

$$\left.\begin{aligned}
P_{\alpha\alpha} &= \frac{R}{2B^2}(\cosh 2\alpha - 1)[2 \sinh 2\alpha - B(1 + \cos 2\beta)] \\
P_{\alpha\beta} &= \frac{R}{2B^2}[2(\cosh 2\alpha - 1) + B \sinh 2\alpha] \sin 2\beta \\
P_{\beta\beta} &= \frac{R}{2B^2}\{2 \sinh 2\alpha(1 - \cos 2\beta) + B[2 \sinh 2\alpha - (\cosh 2\alpha + 1)(1 - \cos 2\beta)]\} \\
\frac{u_\alpha}{h} &= \frac{c^2R}{8\mu}[2(1 - 2\sigma) \cosh 2\alpha - 4(1 - \sigma) \cos 2\beta + 2 \\
&\qquad - \sinh 2\alpha(1 - 2\sigma + \cos 2\beta)] = Ru_2, \quad \text{say} \\
\frac{u_\beta}{h} &= \frac{c^2R}{8\mu}(1 - 2\sigma + \cosh 2\alpha) \sin 2\beta \qquad = Rv_2, \quad \text{say}
\end{aligned}\right\}. \tag{3}$$

If θ as before be used for the angles made by the isostatic surfaces with the hyperbolæ, one obtains from the above formulæ the relation

$$\tan 2\theta = \frac{\sin 2\beta[\mathrm{B}\sinh 2\alpha + 2(\cosh 2\alpha - 1)]}{\mathrm{B}(1 - \cosh 2\alpha\cos 2\beta) - 2(1 - \cos 2\beta)\sinh 2\alpha}.$$

The surfaces so determined are the same as those of fig. 2.

These results may be applied to the theory of intrusion in the manner which follows. Inglis supposes that the crack or elliptical cavity contains only vacuum. If, however, one adds, vectorially, to the displacements of any system, those which correspond to a uniform pressure Q, extending throughout an infinite solid under plane strain, in every direction in the plane, the expressions are still such as will satisfy the equations of equilibrium. The boundary conditions, however, are altered. One must suppose that the cavity is occupied by fluid under pressure Q, while the tensions at infinity are everywhere modified by having the quantity Q subtracted. The forms of the intrusive bodies are not, perhaps, those most likely to occur in reality. The crack, for instance, will be occupied by a sheet intrusion, of a shape which may be compared to that of a steel ruler, whose length is theoretically an infinite number of times its breadth. It seems probable, however, that the results obtained for this case may be applicable in some respects to other sheet intrusions, in particular in regard to the conditions obtaining along the edge.

It is possible, for instance, to investigate the case where a liquid under pressure Q is intruded into a solid which was not previously under pressure or tension. For intrusion into the crack this is done by first substituting Q for R in equations (1). To the value of $\frac{u_\alpha}{h}$ which is so derived, and to the zero value of $\frac{u_\beta}{h}$, one then adds the quantities

$$-\frac{c^2\mathrm{Q}}{4\mu}(1 - 2\sigma)\sinh 2\alpha \quad \text{and} \quad \frac{c^2\mathrm{Q}}{4\mu}(1 - 2\sigma)\sin 2\beta,$$

which correspond to a uniform pressure of amount Q. One thus obtains

$$\frac{u_\alpha}{h} = \frac{c^2\mathrm{Q}}{4\mu}[(1 - 2\sigma)(\cosh 2\alpha - \sinh 2\alpha) - 2(1 - \sigma)\cos 2\beta + 1]$$
$$\frac{u_\beta}{h} = \frac{c^2\mathrm{Q}}{4\mu}(1 - 2\sigma)\sin 2\beta.$$

The tractions $\mathrm{P}_{\alpha\alpha}$ and $\mathrm{P}_{\beta\beta}$ are found by subtracting Q from the corresponding quantities in (1). The value of $\mathrm{P}_{\alpha\beta}$ will be unaltered, as also will the directions of the isostatic surfaces. The latter are shown in fig. 1, which also indicates at certain points the pressures which will be developed across them.

If the liquid, under pressure Q, is intruded into a solid in which there was no pressure or tension in the y direction, but a pressure Q in the x direction, prior to intrusion, the total displacements may be obtained by making the same additions as before to the values of $\frac{u_\alpha}{h}$ and $\frac{u_\beta}{h}$ derived from equations (3). The corresponding isostatic surfaces, and the pressures across them at certain points, are shown in fig. 2.

One may next investigate the more general case in which fluid under pressure is intruded into a crack of the form supposed, in an infinite solid, in which the principal tractions, previous to intrusion, were in the directions of x and y, as already defined, and of z, the dimension perpendicular to the plane. These tractions will be denoted by X, Y and Z, and may be supposed to have any values. The values will be positive when they denote tensions, and negative when they denote pressures, while the fluid pressure will be denoted by the negative quantity A. The tractions will be unaltered at infinity; this forms one boundary condition, the other being that $P_{\alpha\beta}$ shall vanish along the crack, while $P_{\alpha\alpha}$ shall be equal to A. This problem may be solved by supposing the strains in the solid to be formed by the superposition of four different systems, each of which satisfies the equations of equilibrium.

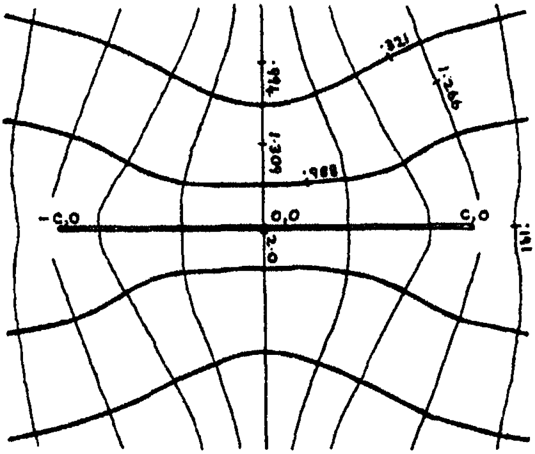

FIG. 2.—Isostatic surfaces. Intrusion into solid previously compressed parallel to fracture.

The first system is given by assuming the displacement u_1, as defined in (1), to be multiplied by a factor which will be denoted as B. In the second one may suppose that u_2, v_2, as given in (3), are multiplied by a factor C. The third consists of an extension which is the same in all directions, and at all points, in the plane, and is sufficient, in itself, to give rise to a plane tension in all directions, equal to D. The fourth system is an extension in the direction of z, which may be denoted as $\frac{\partial w}{\partial z}$, and we define E as being equal to $\frac{2\mu}{(1-2\sigma)}\frac{\partial w}{\partial z}$. The boundary conditions are then given by

$$\left.\begin{array}{l} B+D+\sigma E=X \\ B+C+D+\sigma E=Y \\ 2\sigma B+\sigma C+2\sigma D+(1-\sigma)E=Z \\ D+\sigma E=A \end{array}\right\}.$$

These four simultaneous equations have the solution

$$\begin{aligned} B&=X-A, \\ C&=Y-X, \\ D&=A-\frac{\sigma[Z-\sigma(X+Y)]}{(1-2\sigma)(1+\sigma)}, \\ E&=\frac{Z-\sigma(X+Y)}{(1-2\sigma)(1+\sigma)}, \end{aligned}$$

from which one obtains

$$\left.\begin{array}{l} \frac{u_\alpha}{h}=(X-A)u_1+(Y-X)u_2+\frac{c^2}{4\mu}\left\{A(1-2\sigma)-\frac{\sigma[Z-\sigma(X+Y)]}{1+\sigma}\right\}\sinh 2\alpha \\ \frac{u_\beta}{h}=(Y-X)v_2-\frac{c^2}{4\mu}\left\{A(1-2\sigma)-\frac{\sigma[Z-\sigma(X+Y)]}{1+\sigma}\right\}\sin 2\beta \\ \frac{\partial w}{\partial z}=\frac{Z-\sigma(X+Y)}{2\mu(1+\sigma)} \end{array}\right\}. \quad (4)$$

In (1), (3), and (4) it has been assumed that the ellipse of Inglis's investigation has the limiting form of a straight line, or in other words that $a_0=0$. If a_0 is small, but finite, the tangential tension at the end of the ellipse becomes $\frac{2R}{a_0}$, in the cases corresponding to (1) and (3). This assumes the outline of the cavity to be accurately elliptical, or at least that the extremity has very nearly the form of a parabola. This assumption will not in general be justified.

We may suppose, however, that the cavity connects the two foci, but never extends beyond the narrow elliptical boundaries given by making $a=a_0$. It may be otherwise quite irregular. The stresses in the immediate neighbourhood of the ellipse cannot then be calculated, but at a greater distance it seems certain that they will approximate closely to those given by Inglis's formulæ. If r be the distance from a focus, this will hold even when r is small, so long, at least, as it is of a larger order than ca_0, which represents the semi-axis minor of the ellipse.

This discussion has been introduced because it is important for our purpose to investigate the stresses in the neighbourhood of an extremity. By making a_0 small enough, one obtains the formulæ (1), (3), and (4), and when r is of a larger order than ca_0 the application of these formulæ seems justified. Suppose r to be small, and that θ is the angle made by this radius with the direction of the crack produced. We then have

$$\cosh \alpha = 1 + \frac{r}{2c}(1+\cos\theta),$$
$$\cos \beta = 1 - \frac{r}{2c}(1-\cos\theta).$$

By using the formulæ (1) and (3) it will be found that the displacement $\frac{u_\alpha}{h}=u_1$, $\frac{u_\beta}{h}=0$ gives rise to the stresses

$$\begin{aligned} P_{\alpha\alpha} &= \frac{1}{4}\sqrt{\frac{c}{r}}(1+\cos\theta)^{3/2}, \\ P_{\alpha\beta} &= \frac{1}{4}\sqrt{\frac{c}{r}}\sqrt{(1+\cos\theta)}\cdot\sin\theta, \\ P_{\beta\beta} &= \frac{1}{4}\sqrt{\frac{c}{r}}\sqrt{(1+\cos\theta)}(3-\cos\theta), \end{aligned}$$

while the displacements $\frac{u_\alpha}{h}=u_2$, $\frac{u_\beta}{h}=v_2$ lead to exactly the same result. The remaining terms in the expressions (4) do not correspond to stresses of the same order of magnitude. In the general case, therefore, we have

$$\left.\begin{aligned} P_{\alpha\alpha} &= \frac{Y-A}{4}\sqrt{\frac{c}{r}}(1+\cos\theta)^{3/2}, \\ P_{\alpha\beta} &= \frac{Y-A}{4}\sqrt{\frac{c}{r}}\sqrt{(1+\cos\theta)}\sin\theta, \\ P_{\beta\beta} &= \frac{Y-A}{4}\sqrt{\frac{c}{r}}\sqrt{(1+\cos\theta)}(3-\cos\theta). \end{aligned}\right\} \quad . \quad . \quad . \quad (5)$$

If Y represents a larger pressure than A, Y − A is negative. If this is so, however, the formulæ (4) cannot apply, as u_α would be negative, and clearly, under such circumstances, intrusion cannot take place. If, however, Y represents a tension, or a pressure smaller than A, Y − A is positive, and very large tensile stresses will arise, owing to the fact that c is of a larger order of magnitude than r. This will be the case, even when Y − A is a comparatively small quantity. The tensions will cross the extension, and surround the extremity of the crack. The values of

X and Z, corresponding to the pressures or tensions parallel to the crack, before intrusion, are seen to have no influence on the result.

The directions of the isostatic surfaces, and the relative tensions which cross them at certain points, are shown in fig. 3. The conclusion which has been arrived at may be put into simple language by saying that intrusion, in occupying the blade-like edge of a fissure, must act as a wedge. Proof has only been given for one particular form of fissure, which has here been assumed to be perpendicular to a principal traction in the rock. In all probability, however, the principle is quite general, and will apply to the edge of any intrusive sheet. This is obviously the means by which a dyke or sill is able to extend itself. The only condition is that the intruded magma shall be under a pressure greater than that which is normal to the fissure, in the general body of the rock.

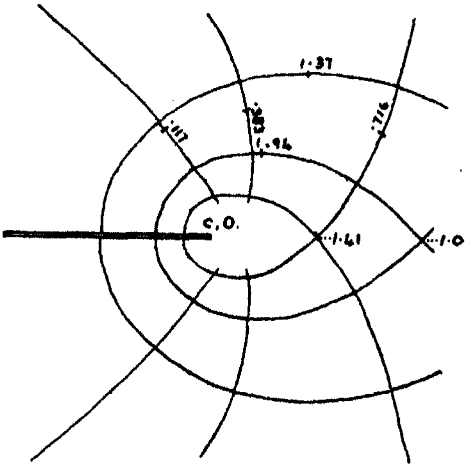

FIG. 3.—Isostatic surfaces close to end of intrusion. Figures show relative tensions across them.

If one of the principal stresses is a tension, intrusion perpendicular to its direction can take place at vanishing pressure. Inglis's researches have shown, in fact, that for the extension of a crack the presence of a magma is unnecessary. This may have a bearing on joint formation. If, on the other hand, a magma is present, an actual tension is not a necessary condition for its intrusion. In a paper previously read to this Society, I have shown that, probably, all three principal stresses were pressures, at the time and place of origin of certain systems of cone-sheets (Anderson, 1936). The same must also apply to sill formation in horizontal strata. The sills must split apart the layers, in spite of a transverse pressure, corresponding to the weight of the overlying rock.

The general process of minor intrusive activity may therefore be regarded as follows. There must, in the first place, be a parent magma reservoir, which may be at a considerable depth within the crust. To explain the origin of the reservoir is beyond the scope of this paper, but it may have the form of a flat sheet, or it may be more or less vertical. One direction of principal pressure will, according to theory, be normal to the margin of the magma. The other two will therefore be parallel to the margin, in its vicinity. If there is pressure in both the latter directions, greater than that of the magma, there can be no wedging effect, and intrusion, if it takes place, must be due to some different mechanism. Suppose, however, that in one or both of these directions there is either tension or pressure less than that of the magma. Consider further what is the probable nature of the margin. It is unlikely that such a boundary, when considered in detail, will be a plane surface. It may be expected to contain irregularities, and some of these may take the form of slits and fissures which, although minute, are large enough to admit the magma. Before penetrating very far, the fluid may begin to exert a wedging action. By this means it extends its fissure, and if the further course runs transverse to a rock pressure which is less than magma pressure the process will continue.

The wedging action will be greatest along those fissures which are most nearly normal to the direction of least principal pressure, or otherwise to the greatest tension, as the tensions which cross the continuation of the crack are a maximum for these fissures. The fissures referred to will therefore tend to be selected. The cone-sheets of any particular system, for instance in Mull, follow parallel, though curving courses, and this shows that the selection is real. The facts have been explained by supposing that there was, in such a case, an underlying dome-shaped magma caldron. The rock-stresses tangential to it were pressures less than that of the magma; they differed also in amount from one another. Intrusion across the direction of greater pressure might be theoretically possible, but it would have given rise to radial dykes, and, in Mull at least, only cone-sheets have been developed. Selection may also be inferred from the fact that regional dyke systems are, in general, more or less parallel.

The "wedging" hypothesis may be taken to give a satisfactory explanation of the inception and development of a sheet-like intrusion. What, however, it may be asked, sets a limit to the continuation of such a sheet? Why, for instance, do not all dykes reach the surface? The answer may be twofold. The pressures or tensions in a rock-body may alter laterally, and they are bound, in certain respects, to alter vertically. The magma pressure may also alter. It will decrease uniformly with height, and there may also, in some cases, be a progressive decrease, connected with the limitation of supply.

An entirely different mechanism must be involved in plutonic intrusion, but the formation of dykes, sills, and cone-sheets may, it is suggested, in most cases be due only to wedging. There are, however, exceptions. These occur when the magma, instead of forming a new fissure, utilizes a fissure or fracture which has been previously formed. This will, in the nature of the case, more probably be a shear fracture than a tensile fracture such as the magma itself would produce. It has been shown that, in all probability, the ring-dykes of Mull and other British plutonic centres occupied such pre-existent fractures (Anderson, 1936), and certain ring-dykes, such as the Loch Bà Felsite, are sheet-like in character. There are also many examples, in the Scottish coalfields, of dykes which have followed previous steeply inclined faults.

The conditions necessary for sheet intrusion may be summed up as follows. There must be a parent magma reservoir, but its vertical or lateral distance from the point considered is not of importance, as long as the following rule is satisfied. The magma must be able to transfer, or raise itself to the point in question, without ever encountering a region in which its own hydrostatic pressure is less than the least principal pressure in the intruded rock. If the fluid forms its own fissure this statement applies without modification. If it follows a pre-existent fracture the words "pressure transverse to the fissure" have to be substituted for "least principal pressure."

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(*Issued separately November* 14, 1938.)

OBITUARY NOTICES.

John Jacob Abel, For. Mem. R.S., Hon. F.R.S.E.

THE death of John Jacob Abel in Baltimore on May 26, 1938, deprived science of an outstanding figure, and colleagues all over the world mourn the loss of a charming personality whose single-hearted devotion to research did so much to establish and advance pharmacology and endocrinology.

He was born in 1857, and received his Ph.B. degree from the University of Michigan in 1883. He studied for a year under Newell Martin at Johns Hopkins University, and then spent seven years of study in the leading Universities of Europe. His teachers included many famous names amongst the founders of modern medical science, *e.g.* Carl Ludwig (physiology), Schmiedeberg (pharmacology), Hoppe Seyler and von Nencki (biochemistry).

In 1893 Abel became Professor of Pharmacology in the Johns Hopkins Medical School, a post which he occupied for nearly forty years until his retirement.

His most famous scientific work was connected with the isolation of hormones. In 1895 he commenced work which resulted in the isolation of the monobenzoyl derivative of adrenaline. As a result of this success others succeeded in isolating the pure crystalline hormone. Nothing had been known previously of the chemical constitution of any endocrine secretion, and hence this work represented a biochemical advance of major importance. Some thirty years later he succeeded in obtaining insulin in crystalline form. These two discoveries are his best-known contributions to medical science, but he was engaged in active research for some fifty years, and his publications deal with problems concerning every aspect of pharmacology.

In addition to his research activities he exercised a great influence as the founder and editor of journals. In 1905 he founded the *Journal of Biological Chemistry*, and in 1909 he founded the *Journal of Pharmacology and Experimental Therapeutics* and subsequently edited it for twenty-three years.

His scientific record, seniority and reputation as an editor naturally conferred on him a great prestige, but these facts do not fully account for the influence he exerted on the development of pharmacology, since this was largely due to his special personal qualities. He combined an enthusiasm for research with an exceptional charm of manner and a special facility for communicating his enthusiasm to younger men. In consequence of this gift there is to-day a long list of persons holding Chairs who commenced their scientific career under Abel.

His international reputation is evidenced by the fact that he held honorary degrees of four American, two British and one Continental University, and was an Honorary Fellow or Member of six American and fourteen foreign scientific societies.

For at least a quarter of a century he was the recognised leader of pharmacology in the United States, and was accorded a very special respect and affection in this country.

See also *Obituary Notices of Fellows of the Royal Society*, vol. ii, 1936–38, pp. 577–581.

A. J. C.

Orlando Charnock Bradley, M.D., D.Sc., F.R.C.V.S.

ORLANDO CHARNOCK BRADLEY was born at Wheelton, near Chorley, in Lancashire, on May 8, 1871.

He received his early education at Wheelton, afterwards proceeding to Chorley Grammar School. Later he attended classes in chemistry, animal physiology and botany at the Harris Institute, Preston, before entering the New Veterinary College, Edinburgh, which was then carried on as a private enterprise by the late Professor William Williams, but was afterwards incorporated by the University of Liverpool in which it now forms the School of Veterinary Science. Bradley's student career was such that his outstanding ability quickly attracted the attention of Williams, and upon his graduating M.R.C.V.S. in 1892 he was at once appointed Lecturer in Comparative Anatomy and in addition was placed in charge of the College Hospital. It cannot be said that his bent ever lay towards clinical veterinary practice, and one may venture to assume that he did not find his hospital duties particularly attractive, especially when they had to be undertaken in conjunction with his studies in comparative anatomy, in which subject, from his first contact with it, he knew he had found his true scientific sphere. It was nevertheless in the field of clinical veterinary medicine that the spirit of inquiry and the faculty of precise observation which he possessed, and in later years so markedly developed, first became evident in a published paper, for it was at this early stage that he recorded his observations on the treatment of intestinal tympany in the horse by antizymotic agents introduced directly into the colon by intestinal puncture.

By reason of temperament and inclination Bradley soon became almost wholly immersed in his anatomical work, and in order (among other reasons) to extend his knowledge of comparative anatomy took up the study of medicine at the University of Edinburgh, where he graduated M.B., Ch.B., in 1900. He was Goodsir Memorial Fellow in the years 1903–5, the title of his thesis being *The Comparative Anatomy of the Mammalian Cerebellum*, and in 1905 was awarded the degree of Doctor of Science in respect of his work on the development and morphology of the mammalian hind-brain. Two years later there followed the conferment of his Doctorate in Medicine for his researches in the development of the mammalian liver, and in 1908 he received from the Royal College of Veterinary Surgeons the John Henry Steel Memorial Medal "in reward of merit."

Between 1893 and 1908 Bradley's contribution to the literature was extensive and during this period he published forty-seven original scientific communications, principally on anatomical, genetical and historical subjects. His text-books have proved of incalculable value to veterinary science. The *Outlines of Veterinary Anatomy* published in three parts in 1896–97 was an immature effort in which he, in after years, found no satisfaction, but his later works were wholly admirable and have become standard texts. These are: *Topographical Anatomy of the Limbs of the Horse* (1920); *Topographical Anatomy of the Thorax and Abdomen of the Horse* (1922); *Topographical Anatomy of the Head and Neck of the Horse* (1923); *Topographical Anatomy of the Dog*, in three editions (1919, 1927, 1935); and *The Structure of the Fowl*, in two editions (1915, 1937).

He founded and was editor of the excellent but short-lived *Veterinary Review* (1917–20), which had as its object the provision of an account of current veterinary literature of interest to the specialist and the practitioner.

In his scientific writings Bradley's diction is simple, clean-cut and explicit, but on occasion he would write, as he would often speak, with grace and charm. His *History of the Edinburgh Veterinary College*, published on the occasion of the centenary of the College in 1923, is not only an authoritative historical record but a fascinating tale.

In October 1900 he was elected to the Chair of Anatomy in the Royal (Dick) Veterinary College and to the Principalship of the College in 1911, in which year he was also appointed to the Barclay and Goodsir Lectureship in Comparative Anatomy in the University of Edinburgh. In the same year he was elected to the Council of the Royal College of Veterinary Surgeons, the governing body of the veterinary profession.

This time not only marked an epoch in Bradley's career, but the circumstances of it effected a widening of his sphere of influence and occasioned a redirection of the main lines of his activities. His research work gave place to administration not only in that which concerned his College, but in the wider field of professional politics. His wisdom in council was early recognised by his being elected Vice-President of the Royal College in 1912, and again in 1919, before proceeding to the Presidential Chair, which he occupied from 1920 to 1922. In 1935 he received the highest honour which it is within the power of the Royal College to bestow—that of Honorary Fellowship.

In 1909 Bradley in a presidential address to the Scottish Metropolitan

Veterinary Medical Society outlined his conception of uniting all the many veterinary societies scattered throughout the country into one national association. At a conference held the following year the principle of amalgamation was approved, and a committee under Bradley's chairmanship was appointed to advance the scheme. After years of labour and in face of much discouragement, approval and acceptance of the constitution and rules of that body now known as the National Veterinary Medical Association of Great Britain and Ireland were finally obtained. Bradley was first elected President in 1914 and served as President continuously until 1922.

The Board of Management of the Royal (Dick) Veterinary College as early as 1907 recognised the need for the removal of the College to new and much more commodious buildings, but because of numerous difficulties and delays the actual building of the new College in Summerhall was not begun till 1913, and its memorial foundation-stone was laid two days before the outbreak of the Great War. The lean years of the war constituted a period during which his dominant qualities, quiet steadfastness to purpose and unswerving determination were most clearly evident. Not only did he find ways and means of carrying on the building of the fabric of the new College in spite of the diminution in the building funds due to the rapidly rising costs, but maintained, at least in being, the National Veterinary Association which almost from its inception he had to guide with a steady hand along the very edge of financial bankruptcy. The fine buildings in which the Edinburgh Veterinary College is now housed and the strength to which the National Veterinary Association has so rapidly attained must have been causes of much satisfaction.

His interest in general scientific matters is reflected in his long association with the Royal Physical Society of Edinburgh, to the Fellowship of which he was elected in 1893, serving as Secretary 1903–11 and as President 1912–15. Between 1901 and 1928 he made twelve contributions to the Society's *Proceedings*.

Bradley was elected a Fellow of the Royal Society of Edinburgh in 1903. He was a member of the Council, 1907–10 and again 1915–17, and served as Vice-President 1934–37. Two of his papers are published in the Society's *Proceedings*: "Abdominal Viscera of *Cercocebus fuliginosus* and *Lagothrix humboldti* (1903), and "Craniometrical Observations on the Skull of *Equus prjevalskii* and other Horses" (1907).

Bradley could upon occasion affect a charming geniality, but his natural manner was placid, suave, precise and even cold. His sense of humour was deep and very real, but his wit, while nimble and adroit, could be sharp. His tastes were artistic and blended curiously but smoothly with his scientific attributes. He performed with acceptance upon the violoncello and appreciated music very warmly; yet, with complete detachment, he could informedly discourse upon the mechanism of its production. He was readily touched by natural beauty, especially the beauty of flowers, and this but served to quicken his interest in the principles and practice of scientific plant-breeding. It was in the possession of so many and such different qualities and of a mind so keen, cultured, and so severally faceted that Bradley was equipped splendidly for carrying through the many important tasks which he sought and to which he set himself. The passage of time alone will permit of the proper assessment of the remarkable contribution he made to the advancement of Veterinary Science during, perhaps, the most critical phase of its development.

He died on November 21, 1937.

J. R. G.

Sir Charles Bright, Kt., M.I.C.E., M.I.E.E.

SIR CHARLES BRIGHT, who died on November 20, 1937, was born in 1863. The son of the man who laid the first Atlantic cable naturally devoted himself to submarine cable work and for some fifteen or more years this claimed his energies, many cables under the oceans being laid or organised by him. But in the invention of wireless telegraphy he recognised the dawn of a new era, and in the early years of the century he became associated with wireless and its application to shipping. He successfully advocated wireless stations round the coast and extended his activities to world radio as the possibilities of the subject developed. His interest in aeronautics led him to apply wireless to ships of the air, as earlier to ships of the sea, and the association with many parts of the Empire through his cable and radio work brought him to other aspects of imperial development, especially trade, industries and patent rights.

With his wide knowledge of other countries he supported the League of Nations, of which he was a Vice-President, and other movements towards peace and amity, and as a keen participator in open-air games and exercise he helped in the promotion of playing fields and athletic clubs. Both his work as a cable engineer and his interest in the Empire made him an extensive traveller, and his experience made him a valuable member of many Government Commissions, including Imperial Relations, Radio-telegraphy, the Dominions, the Royal Flying Corps and Air Congress. These subjects and histories of his father Sir Charles Tilston Bright and of the first Atlantic cable, with contributions to the *Encyclopædia Britannica* and the more important periodicals and technical journals, occupied his pen.

A man of kindly personality, he made many friends. His life was full, fruitful and interesting: such men are the mainstay of their generation.

He was elected a Fellow of this Society in 1895.

F. G. B.

Sir John James Burnet, R.A., R.S.A., LL.D.(Glas.), F.S.A., F.R.I.B.A.

SIR JOHN J. BURNET was the son of an eminent Glasgow architect of the latter decades of the nineteenth century—John Burnet—and became a partner in the firm known for many years as John Burnet & Son. He was born in 1857 in Glasgow and died in Edinburgh on July 2, 1938.

Destined from boyhood to follow his father's profession, he had his preliminary training in the drawing-office of his father after leaving school in Glasgow. After a period he was sent to Paris to continue his artistic and architectural training. There he worked firstly in the studio of Monsieur Pascal and was later admitted to the École des Beaux Arts, where he gained two medals—for mathematics and construction. On returning to Glasgow he resumed work with his father and gained an almost immediate success in a competition for the Galleries of the Royal Glasgow Institute of the Fine Arts. Following this he became increasingly active on succeeding his father, and was responsible for many important buildings in Scotland. Among his principal works are, in Glasgow, the Clyde Trust Offices, extensions to the University and to the Western Infirmary, the Elder Library and the Elder Cottage Hospital in Govan, the Barony Church and the Stock Exchange extensions. Buildings erected after his designs in Edinburgh are the former Professional and Civil Service Stores in George Street, Messrs Forsyth's premises in Princes Street, and the Head Offices of the Union Bank of Scotland, Glasgow. In other parts of Scotland he was responsible for the Gardner Memorial Church, Brechin; the Town Church, Arbroath; the M'Laren Memorial Church, Stenhousemuir; and the restoration of Duart Castle, Mull.

His appointment to be the architect of the King Edward VII Galleries, British Museum extension in 1905, led to many other commissions in the South and was instrumental in the principal offices of the firm being transferred to London. Among his more important works in the capital are the Institute of Chemistry in Russell Square, the Kodak Building in Kingsway, the General Accident Building in Aldwych, Selfridge's extension in Oxford Street, and the conspicuous Adelaide House at London Bridge.

After the war of 1914–18 he was appointed chief architect for the

Imperial War Graves Commission in Palestine and Gallipoli. As senior member of the London firm of Sir John Burnet, Tait and Lorne he gradually retired from business activities and eventually returned to Edinburgh a few years ago, after having lived at Farnham, Surrey.

Sir John was elected a Royal Scottish Academician in 1914 and received a knighthood in the same year, in 1923 the Royal Gold Medal of the Royal Institute of British Architects was conferred on him, and in 1925 he was elected a Member of the Royal Academy. He was an Honorary LL.D. of Glasgow University, a Fellow of the Royal Society of Edinburgh (elected 1887) and a Corresponding Member of the Institut de France, as also of the American Institution of Architects.

Sir John Burnet must be considered as one of the most important architects of this period of transition from the comfortable complacency of the later Victorian decades to the troubled post-war reactions that tend towards a denial of all but functional requirements. The mind of the sensitive and restrained artist, more prominent in the results of his earlier efforts, is nevertheless ever present in the later works in which the more rigid requirements of the times have been dictated to the architect.

In the words used in connection with the conferring of the Gold Medal in 1923, "few architects may be said to have so pervasive an effect on the work of their own time."

Sir John married in 1886 Jean Watt, daughter of the late Sir James Marwick, who was Town Clerk of Glasgow for many years. He is survived by Lady Burnet and had no family.

A. E. H. M.

The Rev. Thomas Burns, C.B.E., D.D.

DR BURNS was a Fellow of the Royal Society of Edinburgh since the year 1888. He was a man of catholic sympathies, unique energy, and very varied gifts. In the fifty years of his ministry in Lady Glenorchy's Parish he found ample room for the exercise of these. In its teeming population dwelt every kind of problem, for in its varied humanity lurked the difficulties of poverty and the slum, though it was not wholly the asylum of the distressed and depraved. He was kept going by a vision which upheld him. He set himself to schemes of education that a door of opportunity might be opened to the children of the poor. In the School Board, on the Heriot Trust, and in the Training College for Teachers he made his practical energies felt. In the interests of the blind he employed all his driving force, with most helpful results. The Royal Blind Asylum and its workshop were in his parish, and many of the blind people had homes and lodgings there, making little of life with their meagre earnings. Work among these gave him his great inspiration after the War, when the difficulties of a sightless population were multiplied. He established Newington House, where the blinded soldiers might be taught to earn their living. And he also founded a home for blind women. For the many-sided activities of a practical religion such as his was, he built a church which was a pioneer in institutional congregational life, and it became a hive of activity. These are his lasting monuments.

He knew intensely the value of education as an uplifting fact, and he was content to make his self-denying labours his best and most eloquent sermons. For the realisation of his humanitarian projects he had no shyness in asking, and I never heard of his receiving a refusal to any appeal he made.

Amidst all his varied activities he made himself a little corner of leisure, in which he wrote his valuable work on *Old Scottish Communion Plate* and other fruits of his archæological knowledge: and he was successful in recovering much forgotten and lost treasure-trove of the Church. He was not confined to any idea of mere parochialism or ecclesiasticism. His interests had a wide stretch in them, but whatever benefits they bore were passed on to the needs of the folk whom he loved to serve. He carried light and a breeze with him, for which many a soul had reason to be thankful. Nothing in his life, work, or thought belonged to a world of standardised humanity or programmed enterprise, yet he was a master of method, and sure of victory, because he had deleted the word "surrender" from his vocabulary of conduct.

He died on January 15, 1938. L. MACL. W.

William Wallace Campbell, For. Mem. R.S., Hon. F.R.S.E.

THE tragic death on June 14, 1938, of William Wallace Campbell removed from the list of Honorary Fellows of the Society a great astronomer and a wise and firm administrator. For over twenty years he was Director of the great Lick Observatory, and it was only as a result of heavy pressure that he consented in 1923 to accept the office of President of the University of California. He had previously refused many important posts on the ground that he preferred the Directorship of Lick to anything else, and even when he was persuaded by a deputation from the University that they were really in need of his outstanding administrative ability, it was his earnest hope that his term of office would be short. He accordingly retained his title of Director of the Observatory in the expectation that he would return to the institution he loved so well, but the task that awaited him was heavy and kept him until his health failed in 1930.

Campbell will remain renowned for his development of the spectroscopic determination of the components of stellar velocities in the line of sight. As early as 1906 his work in this field had earned the Gold Medal of the Royal Astronomical Society, and the Lick Catalogue of Radial Velocities published in 1928 is perhaps the best monument to his memory. This catalogue bears the names of Campbell and of his colleague Moore, and contains the radial velocities of 2760 stars with a complete discussion. The systematic observation of radial velocities has assisted, to a very high degree indeed, the efforts of astronomers to understand the kinematics of the Stellar Universe, and William Wallace Campbell has for long been in the van of this line of research, and has proved himself pre-eminent as an observer, as an organiser, and as one who knew how to extract full information from his observational material. Mention must also be made of his verification, in 1922, of the Einstein gravitational displacement of light, thereby confirming the results of the British observers in 1919.

Campbell joined the staff of Lick in 1891 and became Director in 1901. The success of his work is directly due to his high instrumental skill. Prior to his appointment as Director he set himself the task of designing a spectrograph for the specific purpose of determining radial velocities with all possible accuracy. Thanks to the generosity of Dr D. H. Mills funds were available, and the Mills spectrograph exceeded all expectations, incorporating as it did freedom from flexure, provision for accurate guiding and efficient temperature control. Between August 1896 and August 1898 several hundred spectra were obtained, and the radial velocities of some fifty stars were measured with hitherto unprecedented accuracy. But Campbell was not satisfied, and, utilising Wright's suggestions, for the further elimination of residual flexure, he proceeded to the design of improved Mills spectrographs. By 1909 he was able to determine the solar motion from the radial velocities of 1047 stars, and at the same time made the surprising discovery of what is known as the K Term. In subsequent years the work of measuring radial velocities of stars was pushed steadily forward, but Campbell found time for important spectroscopic researches on Planetary Nebulæ, Novæ, Wolf Rayet stars, the Orion Nebula, and the composition of the atmosphere of Mars. An important by-product of the radial velocity programme was the discovery of the high percentage of close binary star systems existing among the stars.

Even in an abbreviated notice mention must be made of Campbell's eclipse work and his contributions to the study of the Solar Chromosphere. He took part in seven eclipse expeditions and designed a simplified equatorial mounting which was sufficient for the restricted movements needed. An essential feature of the design was its portability, and it has been adopted by many other astronomers. He also introduced a new feature into the photography of the flash spectrum whereby the spectrum of the Sun's edge was recorded continuously for a few seconds at the commencement or end of totality by means of plate-holders moving at a uniform rate by clockwork. This device exhibits very strikingly the different depths at which different Fraunhofer lines are reversed.

In spite of increasing blindness and failing health, Campbell accepted the Presidency of the National Academy of Sciences from 1931 to 1935. The work was exacting and he had to move to Washington. He devoted himself to maintaining the prestige of the Academy, and was instrumental in the creation within the Academy, on the invitation of the President of the United States, of the Government Relations and Scientific Advisory Committee, a body which advises the President and various Government departments on scientific matters. The National Academy of Sciences profited to a considerable degree from their President's high executive ability and tenacity, and his end is the passing of one who, in addition to being a great astronomical pioneer, played an important part in American scientific and academical life.

He was elected an Honorary Fellow of the Society in 1920.

See also *Obituary Notices of Fellows of the Royal Society*, vol. ii, 1936–38, pp. 613–619.

W. M. H. G.

William Eagle Clarke, I.S.O., LL.D.

To the study of the vertebrate fauna of Scotland, and particularly of its birds, Dr Eagle Clarke made many contributions. That was an interesting development for a youth, born in Leeds in 1853, who had been trained as a civil engineer, and it was partly due to an inherent love of nature and partly to the influence of a great teacher of zoology, Professor L. C. Miall, under whom Eagle Clarke studied at the Yorkshire College, which became the University of Leeds.

A definite trend was given to his life's work when at the age of thirty-one he was appointed Curator of the Leeds (Philosophical Society's) Museum, and its direction was fixed when four years later, in 1888, he was made Assistant in the Natural History Department of the Museum of Science and Art (now the Royal Scottish Museum) in Edinburgh, under its first independent Keeper, Dr Ramsay H. Traquair. The great part of his working life was spent in that institution, where he succeeded Dr Traquair as Keeper in 1906, and from which he retired in 1921. There he made many changes, developing the collections for the use of students, encouraging the popular aspect of the exhibits, and bringing together by the way one of the finest exhibited collections and cabinets of British birds in the country.

Dr Clarke's scientific work covered a wide field in systematic zoology, ranging through all the classes of vertebrates, as witness his papers on the fishes of the Forth and its tributaries or his description of new forms of small mammals from the islands. But his name will be linked particularly with the study of birds, and there especially with the phenomena of migration. He added, perhaps more than any other, to the list of those rare birds which make an occasional appearance in Scotland. In Europe he found fresh material for publication in tracking the birds of Brabant, of Slavonia and Hungary, of Iceland and the Faroes, of the Pyrenees and the delta of the Rhône. Still further afield he identified collections of birds from the northern islands of Jan Mayen and Franz Josef Land, from Hudson's Bay, from the tropical Philippines, and from the Antarctic voyage of the *Scotia*.

His contributions to our knowledge of the migrations of birds are outstanding. Appointed a Member of the British Association Bird Migration Committee in 1880, he drew up its final Reports, and in the course of collecting information he developed two effective methods of studying migration. By living in lighthouses and lightships and by enlisting the services of light-keepers he was able to catch bird movements in full swing, and his repeated visits during seasons of migration to Fair Isle, isolated between the Orkney and Shetland Islands, gave that tiny island something of the bird-watching fame which Gätke's fifty years of observation gave to Heligoland. The results of his observations appeared in final form in two volumes, *Studies in Bird Migration* (1912).

In addition to these volumes he published, with W. D. Roebuck, *A Handbook of Yorkshire Vertebrata* (1881); with J. G. Bartholomew and Percy H. Grimshaw an *Atlas of Zoogeography* (1911); edited Colonel Wardlaw Ramsay's posthumous *Birds of Europe and North Africa* (1923); and rewrote Howard Saunders' *Manual of British Birds* (1927).

For forty years he acted as editor or as joint-editor of *The Scottish Naturalist* and its predecessor *The Annals of Scottish Natural History*, and in that capacity he guided to a great extent the development of field natural history in Scotland.

Dr Clarke's work gained him many marks of recognition. He was created a Member of the Imperial Service Order in 1920; the University of St Andrews conferred on him the degree of LL.D.; in 1918 he was elected President of the British Ornithological Union, and in 1922 he was made the first recipient of the Godwin-Salvin Medal. He was an honorary member of many foreign ornithological societies, and in this country he took part in several commissions concerned with wild birds and their protection, a subject upon which he acted as adviser to the Scottish Office for many years in connection with the administration of the Wild Birds Protection Acts.

Dr Clarke's holiday pursuits were angling and walking, and it was a great pleasure to share an outing with an observer so skilled and so well versed in field natural history. That was a study he did much to stimulate in Scotland, and many owe their interest in Scottish animals to his enthusiasm and kindly encouragement. He died, after a long period of failing health, on May 10, 1938, in his eighty-sixth year.

He was elected a Fellow of this Society in 1903.

J. R.

Sir James Crichton-Browne, M.D., LL.D., D.Sc., F.R.S.

ON January 31, 1938, Sir James Crichton-Browne died a few months after his 97th birthday. In him the Royal Society of Edinburgh lost its oldest Fellow, for he was elected in 1870. He held a similar distinction in the Royal Society, to which he was elected in 1883.

His father, Dr W. A. F. Browne, who was the first Medical Superintendent of the Crichton Royal Mental Hospital at Dumfries, was largely responsible for the high standard of care and treatment of the insane for which this institution has since been famous; later he became Commissioner in Lunacy in Scotland. It was therefore not surprising that after qualifying in medicine in Edinburgh University at the age of 22, his son decided to devote himself to the study of mental disorders. After serving in junior posts in various county mental hospitals he was appointed in 1866 Medical Superintendent of the West Riding Asylum at Wakefield, a post he held until 1875. It was here his most valuable researches and pioneering work were done. On obtaining the independence and the opportunities for study which his new post gave him, Crichton-Browne at once attempted to initiate an investigation of mental disease on a scale which had not been previously adopted in this country.

As facilities for the publication of papers on neurological and psychiatric subjects were then very limited, Crichton-Browne also instituted, in 1871, the West Riding Asylum Reports, in which there appeared under his own direction and that of his successors several valuable contributions to this branch of medicine from both members of his staff and from others who were interested in his venture, as Ferrier, Hughlings Jackson, Clifford Allbutt, William Turner the anatomist, and others. As a result of these activities the Wakefield Asylum became a recognised centre for the study of the brain and its disorders; and though its superintendent was unable, owing to his official duties, to devote much time to original investigation, his enthusiasm and critical mind stimulated and guided the work which was undertaken in the wards and laboratories of the Hospital.

In 1875 he was appointed Lord Chancellor's Visitor in Lunacy, and he was compelled to move to London. His new post gave him little opportunity for study or research, but his interests remained unabated. He was responsible, in conjunction with Hughlings Jackson and David Ferrier, for the foundation in 1878 of the neurological journal *Brain*, and he was for a time co-editor of it. The most noteworthy of his own contributions to it was on "The Nature and Cortical Localisation of Muscle Sense," which revealed his power of accurate observation. He soon became a member of the Royal Institution, of which he was for many years Treasurer, and later a Vice-President; here he had opportunities of keeping in contact with various branches of scientific work; in fact, the affairs of the Institution were for long his chief interest outside his professional life.

His post as Visitor in Lunacy enabled him to emphasise his views on the importance of the early treatment of mental disorders, but he had to recognise the inadequate responses to his efforts from both official circles and from the medical profession; in this matter he was before his time. In 1884 he presented an important report on the influence of primary education on mental health and development and on the effect of overwork in the elementary schools, which at that time attracted considerable attention, and was printed for circulation by order of the House of Commons.

Crichton-Browne was an eloquent and a popular lecturer, and until recent years spoke frequently before various audiences on psychology and allied medical subjects, especially in their social relations. To later generations he was known chiefly as a gifted orator, and he was particularly famous as an after-dinner speaker. He published several volumes of reminiscences under the title *Leaves from a Doctor's Diary*, which attained considerable popularity. Till his end he retained his activity of mind and body, and to many of his friends he seemed to possess the secret of perpetual youth.

Crichton-Browne was knighted in 1886; he received the honorary degree of D.Sc. from the University of Leeds, and that of the LL.D. from Aberdeen and Edinburgh. He was in succession President of the Royal Medical-Psychological Association, of the Neurological Society, and of the Medical Society of London.

By his first wife, a daughter of Dr J. Halliday of Seacombe, he had a daughter who survived him and a son whose death preceded his own by only a few months. In 1912 he married a daughter of General Sir E. G. Bulmer, who survives him.

(Condensed from the *Obituary Notices of Fellows of the Royal Society*, vol. ii, 1936–38, pp. 519–521, by permission.)

Alexander John Dey.

Mr Dey was born at Rothiemay in Banffshire and served his apprenticeship there as a pharmaceutical chemist with Messrs Pirie & Sons. After a short period in Aberdeen he came to Edinburgh in 1887 and continued his studies at the Royal Dispensary School of Chemistry ("Duncan's") and qualified as a pharmaceutical chemist in 1890. In 1892 he joined the staff of Messrs T. & H. Smith, the well-known manufacturing chemists, becoming Manager in 1899 and a Director in 1904.

He was actively concerned with the development of the firm's business, and was responsible for the removal of the works in 1906 to a much larger site on the outskirts of Edinburgh, the old name of the Blandfield Chemical Works being retained. Since then large additions to the works have been carried out under his direction.

The War made great demands on the products of the firm, and Mr Dey undoubtedly suffered in health from the strain of these years. He retired in 1935, much to the regret of his colleagues and staff.

Mr Dey was elected a Fellow of the Royal Society of Edinburgh in 1925.

In his early days he was much interested in curling, and he was also a keen fisherman.

He died in Edinburgh on December 19, 1937, at the age of sixty-nine. His death removes a man of much administrative ability, and his loss is regretted by a large circle of friends.

A. L.

Alexander Galt, D.Sc.

ALEXANDER GALT was born in Mauchline in the year 1854. He was educated at Kilmarnock Academy and later received a very thorough and comprehensive training at Glasgow Training College, Glasgow University and the City and Guilds Institute, London. He graduated B.Sc. in Glasgow in 1887 and received his doctorate in 1898. He held various teaching posts before becoming official assistant to Lord Kelvin at Glasgow University. While at Glasgow University Dr Galt had excellent opportunities of engaging in research, and presented papers, both alone and jointly with Lord Kelvin, to the Royal Societies of London and Edinburgh. He left Glasgow to organise the science training in the Episcopal Church Training College in Edinburgh.

In 1901 the control of the Royal Scottish Museum was transferred from the Science and Art Department, London, to the Scottish Education Department, and Sir Francis Ogilvie, at that time director, appointed Dr Galt to organise a new department of the museum—the Technological Department—which was to be closely associated with the technical education in Scotland. Dr Galt's wide educational experience fitted him admirably for his new work, which he developed with the happiest results till his retiral under the age limit in 1920.

He was elected a Fellow of this Society in 1887, and died at Mont Felard in the Channel Islands on June 26, 1938, in his eighty-third year.

T. R.

George Ellery Hale, For. Mem. R.S., Hon. F.R.S.E.

By the death, on February 22, 1938, of George Ellery Hale, astronomy has lost one who notably influenced the progress of the science, both by his outstanding powers of organisation and by his individual researches. The Observatories of Yerkes and Mount Wilson remain as monuments to the memory of Hale the organiser, and a long record of published research has been recognised by many honours, including the award of the Royal Astronomical Society's Gold Medal in 1904, and the Copley Medal of the Royal Society in 1932.

Hale was born in Chicago on June 29, 1868. His interest in practical astronomy dates from his boyhood, when with the aid of a small grating spectroscope he observed the solar spectrum, and compared it with flame and arc spectra. He entered the Massachusetts Institute of Technology in 1886 and graduated in 1890. During this period he officially studied mathematics, physics and chemistry, but he found time to serve as a volunteer assistant at Harvard Observatory, and tried out his first spectroheliograph in 1889. This was the forerunner of the perfected instrument, the completion of which was announced in 1892, and which provided a means of photographing the sun's disc in monochromatic light. In the hands of Hale himself, Deslandres and others it has proved to be an effective instrument of research, and the production of it alone would rank as an instrumental achievement of the highest order.

After his graduation, Hale was offered the opportunity of developing his spectroheliograph at Lick Observatory. He declined this offer, and established with the aid of his father a private observatory at Kenwood, in a suburb of Chicago. In 1891 he photographed the spectrum of a prominence, being the first to do this without the aid of an eclipse. Important studies of the whole solar disc, using his newly perfected spectroheliograph, were carried out at about this time, and Hale discovered the presence of large bright calcium flocculi on the disc, particularly around sunspots.

The three years' research at Kenwood were interrupted by a visit to Europe in 1891, where Hale met many astronomers and spectroscopists and studied their equipment. He spent the winter of 1893–94 at Berlin, where he attended Planck's lectures on thermodynamics. But his private research at Kenwood was destined to be of short duration. In 1892 his pioneer work had won him recognition by the University of Chicago, of which he became an Associate Professor of Astrophysics. With the backing and help of the President of the University he formed plans for the building of a great observatory, and eventually Mr Yerkes, a Chicago millionaire, was persuaded by President Harper and Hale to provide the funds. The Yerkes Observatory was completed in 1897, and Hale surrounded himself with a talented staff including Barnard, Burnham, Wadsworth, Frost and Ellerman.

The foundation and development of an observatory such as Yerkes was in itself an achievement which could only be carried through by a man combining exceptional powers of organisation with high technical ability. But a greater task was in store. In the winter of 1903–4 Hale was in southern California owing to illness in his family, and he found time to make tests of the conditions prevailing on Mount Wilson. He recognised the astronomical value of the site, and with the aid of a grant from the Carnegie Institution of Washington an expedition came from Yerkes and set up the Snow horizontal telescope, consisting of a large spectrograph and long-focus concave mirror fed by a cœlostat. The Carnegie Institution then decided to finance a new observatory, and in December 1904 the Snow telescope was purchased from Yerkes.

So began the world-famous Mount Wilson Observatory. Expansion of its activities was rapid under Hale's leadership. The 60-foot and 150-foot tower telescopes were designed and erected, and the work of the new observatory, which at first was devoted to solar research, expanded into the domains of stellar astronomy, the 60-inch reflector being followed by the 100-inch Hooker telescope which was eventually completed in 1919. Hale remained Director till 1923 and then was compelled to retire owing to reasons of health. He erected for himself a small private observatory for solar research in Pasadena, and it was there that he designed and perfected the spectrohelioscope, an instrument allowing an observer to obtain a visual image of the solar disc in monochromatic light. It was soon realised that here was an instrument ideally designed for the study of short-lived chromospheric phenomena, and the first-fruits of the new instrument lie in the recognition, by its aid, of intense transient bright flocculi in hydrogen light and of their correlation with ionospheric disturbances.

During the last years of his life Hale played a prominent part in the plans for the new 200-inch telescope, now in process of completion, and while it is a matter for deep regret that he has not survived to see this instrument in use, it is some consolation to know that its progress was far enough advanced for him to realise that the battle was won, and that the instrument was assured of coming into active use.

We must now turn to Hale's individual contributions to research. The majority of his papers are to be found in the publications of the Yerkes and Mount Wilson Observatories and in the *Astrophysical Journal.* We select for special comment the researches carried out by himself and his colleagues on Solar Magnetic Fields. In 1908 he discovered unmistakable evidence of a Zeeman effect in the sunspot spectrum, the components of the doubled iron lines being shown, by the use of a Fresnel rhomb and Nicol prism, to be circularly polarised in opposite directions. The existence of strong magnetic fields in sunspots of the order of 3000 gausses was thus established. Later researches revealed a wealth of interesting phenomena. It was found that the two members of a bipolar spot group have opposite magnetic polarities, that the polarities of the preceding and following members have opposite polarities in the northern and southern solar hemispheres, and that the whole polarity scheme reverses for successive sunspot cycles. These and other beautiful results achieved by the enthusiasm, skill and patience which were characteristic of Hale, and which he knew well how to induce in his colleagues, present the theoretical astrophysicist of to-day with some extremely interesting—and extremely difficult—problems.

A further problem was tackled—the possible existence of a general magnetic field of the Sun as shown by the Zeeman effect. The field, if any, is relatively small and the task of measurement very difficult. The measurements of 1909 and 1910 indicated a maximum field strength of the order of fifty gausses, but later measurements suggest smaller values. The present position may be stated thus—there is a presumption for the existence of the field, but complete and definite proof is still lacking.

Hale's success was due in no small measure to his personality. The fact that he was able to get men like Yerkes and Hooker to finance his schemes speaks for the confidence which he always inspired in others. He possessed a capacity for surrounding himself with highly efficient colleagues, and for obtaining their esteem and affection, which were shared by astronomers in all countries of the world. The news of his death, which took place on February 22, 1938, at Pasadena, was received with universal regret.

His scientific activities extended beyond his own research work and the affairs of the observatories he founded. In conjunction with James E. Keeler he founded the *Astrophysical Journal* in 1895. It was on his initiative that the International Solar Union was founded in 1904, and when the work of this body was eventually merged in the wider activities of the International Astronomical Union he became President of the Commission of Solar Physics. He was Foreign Secretary of the National Academy of Sciences and was active in establishing the National Research Council of the United States. In 1919 the International Research Council was formed, and Hale was naturally and inevitably an active member of the original executive. In the last years of his life he became President (1934–37) of the International Council of Scientific Unions.

He was elected an Honorary Fellow of the Society in 1913.

See also *Obituary Notices of Fellows of the Royal Society*, vol. ii, 1936–38, pp. 523–529.

W. M. H. G.

Sir William Campbell Johnston, W.S., LL.D.

SIR WILLIAM CAMPBELL JOHNSTON, who died on October 6, 1938, was the last survivor in his generation of a distinguished family which included the Hon. Lord Johnston, Col. Sir Duncan Johnston, K.C.M.G., C.B., Director-General of the Ordnance Survey, and Dr Mackenzie Johnston. He was born in 1860, his father being Henry Johnston, surgeon in the Honourable East India Company's service. After completing his education at Clifton College he was apprenticed as a W.S. and was admitted to membership of the Society in 1885.

He rapidly made a name for himself in legal circles and took an active part in the councils of the W.S. Society. In 1922 he became Collector of the Widows Fund, and was appointed Deputy Keeper of the Signet in 1924 on the resignation of Sir George Paul—an office which he held until his resignation in 1935. He received the Honorary Degree of LL.D. from the University of Edinburgh in 1928 and was knighted in 1934. He was admitted to the Fellowship of the Society in 1934.

He was the trusted adviser of a large circle of clients and held many important legal appointments. He was also a Director of many important financial institutions, amongst them the Commercial Bank of Scotland Ltd. and the Life Association of Scotland. Keenly interested in education, he was a Governor of Fettes College and of Keil College, Dumbarton, and was Clerk to the Governors of Morrisons Academy, Crieff. He had also a close interest in John Watson's School for fatherless children, the Governors of which are the Keeper and Commissioners of the Signet. All these institutions owed much to his guidance.

During his tenure of office as Deputy Keeper important legal developments took place, in which he had a large part. One of these was the passing of the Solicitors (Scotland) Act, 1933, which set up the General Council of Solicitors as the governing body of solicitors in Scotland. He was elected the first Chairman of this body, and the smoothness with which the new machinery worked was largely due to his genius for obtaining the collaboration of others and to the universal respect in which he was held.

Sir William had many interests other than purely professional. He was a member of the King's Bodyguard for Scotland (Royal Company of Archers). In his younger days he was a noted cricketer, but in later years golf was his main recreation.

Predominant amongst his interests, however, was the W.S. Society, and the affection with which he was regarded was evidenced in 1932 when members of the Society subscribed for his portrait which now hangs in the rooms of the Society, and again in 1934 when he was entertained at a banquet in the Parliament Hall by members of the Society.

E. M. W.

Sir Colin Mackenzie, M.D., F.R.C.S.Ed.

COLIN MACKENZIE was born of Scottish parents at Kilmore, Victoria, in 1877. One of four brothers educated for the medical profession, he graduated M.B. at the University of Melbourne in 1898 and M.D. in 1901. In the early years of his professional life he had experience of general practice, but the lines of his career were soon determined by teaching appointments in Anatomy at the University of Melbourne and a clinical appointment at the Children's Hospital in that city.

In 1904 he visited Europe to pursue orthopædic studies, and worked for some time with Robert Jones at Liverpool. Faced with a severe epidemic of infantile paralysis soon after his return to Melbourne, he devised new methods of treatment for the immediate and remote effects of that crippling malady.

Success in specialist orthopædic practice followed, but meanwhile Mackenzie had taken up an intensive study of the comparative anatomy of the peculiar fauna of Australia from the point of view of the correlation of structure and function. To this work he devoted all his spare time and began to build up a great collection of dissections.

During the War he worked in London, and was for a time actively associated with the treatment of war injuries, in charge of a special department in the Military Orthopædic Hospital at Shepherd's Bush.

Thereafter Mackenzie devoted himself finally to the comparative anatomy of the Australian fauna, and in 1924 the dream which had inspired him for many years was realised. In that year he presented to the Federal Government his great private collection of specimens and dissections, and a special Act was passed establishing the Australian Institute of Anatomy. He was appointed the first Director and in 1930 his collection, now greatly augmented by the addition of anthropological and other material, was transferred to the monumental building which had been erected to receive it. It will assuredly be a lasting memorial to Mackenzie's vision, industry and tenacity of purpose.

His well-known book on *The Action of Muscles, including Muscle Rest and Re-education* was published in 1918; *Intellectual Development and the Erect Posture* followed in 1924; and he also recorded his observations on the *Comparative Anatomy of the Australian Fauna* in four volumes.

He received the honour of Knighthood in 1929. He had been President of the Royal Zoological Society of Victoria, and in 1928 was Bancroft Lecturer and President of the Zoological Section of the Australian Science Congress. In 1937 he was elected the first President of the Royal Society of Australia.

Sir Colin Mackenzie died in Australia on June 29, 1938, a few months after he had resigned his post of Director of the Institute of Anatomy on account of ill-health. He was elected a Fellow of this Society in 1905.

J. C. B.

Sir David Orme Masson, K.B.E., D.Sc., LL.D., F.R.S.

SIR DAVID ORME MASSON, who died at Melbourne as Professor Emeritus of the University there on August 10, 1937, at the age of 79, had been a Fellow of this Society since 1885. He was born in London in 1858, and at an early age he accompanied his parents to Edinburgh on the appointment of his father, the late Professor David Masson, to the Regius Chair of English in the University. After four years' school education at the Edinburgh Academy he became, at the age of 15, a matriculated student of the University in the Faculty of Arts, and during the succeeding four years, besides taking other classes, he attended those of Mathematics with Kelland, Greek with Blackie, Natural Philosophy with Tait, and Chemistry with Crum Brown, and he received various class honours. He obtained the degrees of M.A. in 1877, B.Sc. in 1880, and D.Sc. in 1884, his thesis for the latter degree being entitled "The Nitrous and Nitric Ethers of Glyceryl." He was appointed to the Chair of Chemistry in the University of Melbourne in 1886.

After obtaining his degree in science he spent some time at Göttingen with Wöhler and Hübner, and was for a short period an assistant with Professor William Ramsay at Bristol. Thereafter he returned to Edinburgh, where he remained for about four years. This ante-Melbourne period was characterised by much youthful ardour and general buoyancy of spirits, which found congenial outlets in connection with the Tercentenary Celebrations of Edinburgh University, and in enthusiastic activity incidental to the founding of the Students' Representative Council and the Students' Union. Side by side with these various interests Masson carried on chemical research work in Crum Brown's laboratory, partly in collaboration and partly on subjects chosen by himself. The present writer possesses, bottled and labelled, specimen products of the former, and carries on his brow some indelible records of the latter that were conspicuously visible for more than a year and are still recognisable after fifty years. In retrospect upon this period, fadeless memories present themselves of a genial friendship associated with a charm of manner and a grace of diction that are seldom surpassed.

Shortly before leaving for Australia, Masson was married to Miss Mary Struthers, second daughter of Professor Sir John Struthers, M.D., of Aberdeen.

(See also *Obituary Notices of the Fellows of the Royal Society*, vol. ii, 1936–38, pp. 455–464.)

L. D.

William Carstairs Reid, M.Inst.C.E.

MR WILLIAM CARSTAIRS REID, M.Inst.C.E., died on October 29, 1937. At the time of his death he was Senior Partner of Messrs J. & A. Leslie & Reid, C.E., which firm for nearly one hundred years has been responsible for the construction of many important engineering works in Scotland, chiefly in connection with Water Supplies.

Mr Reid's grandfather, the late Mr James Leslie, acted as Engineer for the Edinburgh Water Company, and in that capacity constructed the North Pentland Reservoirs. Mr Reid's father, the late Mr Robert Carstairs Reid, as a partner in the firm, took a leading part in the design and construction of the Moorfoot Scheme, which involved the construction of four large reservoirs.

Mr William Carstairs Reid attended Engineering Classes at the University of Edinburgh, and after an office training acted as Resident Engineer on the construction of Talla Water Works, the largest of the schemes for supplying water to Edinburgh. Mr Reid was assumed as a partner in the firm in 1905, shortly after the completion of the Talla Works. He was associated with the Edinburgh Water Undertaking for nearly forty years, and for over twenty-five years represented his firm in acting as Engineer of the Edinburgh Water Undertaking. This period saw great expansion of the city, and many important extensions of the Water Works were carried out under Mr Reid's direction involving an expenditure of nearly one million pounds.

Mr Reid was frequently consulted by other Water Authorities throughout Scotland and was also called upon to act as arbiter in many important cases. He had an extensive knowledge of Waterworks Administration and Law, and in the consolidation of the Edinburgh Water Acts into the Edinburgh Corporation Order 1924 he assisted the town very extensively in compiling this Order.

While Mr Reid was a partner, the firm of Messrs Leslie & Reid carried out many Water Schemes, of which those in connection with the Kirkcaldy District of Fife, Bathgate District of West Lothian, and Stirlingshire and Falkirk were the most important and involved expenditure of over £1,200,000.

Mr Reid was unmarried. He was much liked by a large circle of friends and employees with whom he came in contact. His principal recreations were fishing and golf.

He was elected a Fellow of this Society in 1924.

P. B. G.

Hon. Alexander William Roberts, D.Sc., F.R.A.S.

ALEXANDER WILLIAM ROBERTS was born at Farr, in Sutherland, of a crofter family, on December 4, 1858. His father was of Irish extraction, but on the maternal side he claimed descent from the Gordons of Huntly. His parents came south in 1864 and settled in Leith. A "lad o' pairts," Roberts was destined for the teaching profession and received his education at Moray House, then the Free Church College for the training of teachers, and at the Heriot-Watt College. From boyhood he had been keenly interested in astronomy, and in 1878 he applied to Piazzi Smyth, then Astronomer Royal for Scotland, for an assistantship in the Royal Observatory. Piazzi Smyth for some reason or other dissuaded him from adopting the career of a professional astronomer, and he accepted a teaching appointment at Wick. Three years later he returned to Edinburgh and entered the University. In 1883 he accepted a post on the teaching staff of the Free Church Mission College at Lovedale, Cape Colony, which position he retained for many years. He was a devoted missionary teacher, and became a recognised authority on native questions. His appointment as a Senator of the Union of South Africa was in itself a tribute to his wide knowledge of affairs and also to Lovedale College.

Throughout his strenuous career Roberts retained his early love for astronomy. Soon after he settled at Lovedale he began observation of the southern skies. He erected a small private observatory, and in 1891 commenced a systematic search for variable stars, which was rewarded within four years by twenty discoveries. Later he concentrated on the study of eclipsing variables, more especially RR Centauri, one of his own discoveries, and V Puppis. Roberts was a pioneer in the study of eclipsing variables, and from the light-curves of these two stars he succeeded in getting approximate elements of their orbits, masses and densities. Roberts was a visual observer only, working with neither spectroscopic, photometric or photographic aid, and his friend Sir David Gill did not exaggerate when he said that he knew "few instances of more successful devotion of small means and limited opportunity to the attainment of great scientific ends than the work of Dr Roberts." The excellence of his work was recognised by the degree of Doctor of Science conferred by the Cape University.

Roberts was a man of varied interests and charming personality. He was elected a Fellow of this Society in 1898, and died at Alice, Cape Observatory, on January 27, 1938, in his eightieth year.

H. M.

David Alan Stevenson, B.Sc., M.Inst.C.E.

DAVID ALAN STEVENSON, eldest son of David Stevenson, B.Sc., M.Inst.C.E. (1815–86), was born in Edinburgh on July 21, 1854. He was educated at the Edinburgh Academy and the University of Edinburgh, where he graduated B.Sc. in Engineering in 1875. A fellow-student was the late Principal Sir James Alfred Ewing. It was while staying at North Berwick in his boyhood days that he and his cousin, Robert Louis Stevenson, rambled over the "Bents" as far as Archerfield Summer House, the venue of *The Pavilion on the Links* which "R. L. S." inscribed to him "in memory of days near Fidra." It was here also, in Mr Stevenson's own words, that "in dark evenings we wandered about with lanterns, burning our fingers and polluting the atmosphere with the smell of burnt oil and hot metal," which episodes are described in *The Lantern Bearers.*

He was initiated into practical engineering by visiting various works in progress, including Anstruther Harbour and Dhu Heartach Lighthouse. His pupilage was served in the office of his father and his uncle Thomas Stevenson. In 1877 he visited the United States and Canada for the purpose of studying the principal engineering works of these countries.

In 1885 Mr Stevenson was appointed joint Engineer to the Commissioners of Northern Lighthouses with his uncle, and on the death of the latter in 1887 he was appointed sole Engineer to the Commissioners. During his tenure of office he was responsible for the design and construction of 24 lighthouses, 48 fog-signal installations, 33 of which were powerful sirens, one manned light-vessel, 4 unmanned light-vessels, 75 unattended minor lights and numerous beacons and buoys on and around the coasts of Scotland and the Isle of Man. There have also been established 7 radio beacons, and 16 isolated lighthouse stations have been equipped with wireless telephones. Among the lighthouses, special mention may be made of Sule Skerry, Flannan Islands, Bass Rock, Oigh Sgeir, Stroma, and Rattray Head, all works presenting difficulties requiring the exercise of sound judgment and engineering skill. The two fog-signals on Ailsa Craig (1886) were the first to be operated at long distances from the power source and the attendants, and Rattray Head (1896) was the first instance of a first-class siren fog-signal being installed in a rock lighthouse. As far back as 1898, when Flannan Islands Lighthouse was being built, he gave serious thought to the possibility of maintaining communication with the shore by means of wireless telegraphy, and in 1904 he was considering the possibility of employing wireless for warning shipping during fog.

In 1883 Mr Joseph Chamberlain, then President of the Board of Trade, was interested in a discussion that was going on as to whether oil, gas, or electricity was the best illuminant for lighthouses, and he had an interview on this subject with Mr Stevenson, acting for Mr Thomas Stevenson. An electric light was subsequently installed at the Isle of May. To the Institution of Mechanical Engineers he, in 1887, read a paper giving an account of this electric light installation.

The firm of D. & C. Stevenson, of which Mr Stevenson was senior partner, was founded by his grandfather, Robert Stevenson, in 1785. Their advice was much sought in connection with River Improvement and Harbour Works in this and other countries. They acted as Engineers to the Clyde Lighthouses Trustees and were Consulting Engineers to several Colonial and Foreign Lighthouse Authorities. Mr Stevenson, in conjunction with his brother, introduced many important improvements into the lighting and fog-signalling of our coasts.

His firm was employed in connection with a project to connect the Forth and the Clyde by a ship-canal. They recommended the route by Loch Lomond, and Parliamentary plans were prepared, but the promoters felt they could not proceed without Government assistance. It was this scheme which the Government of the day (1909) and the Defence Committee considered was the only one that they might assist financially. Among the many notable works carried out by his firm, mention may be made of an unattended lighthouse with a powerful siren fog-signal on a low-lying rock named Platte Fougère near the entrance to St Peter Port, Guernsey, completed in 1910. The air compressors on the rock tower are operated by electric motors, the current being supplied from the shore station at Doyle Fort, distant 1½ mile, by means of a submarine cable.

Mr Stevenson was extra-mural examiner in Engineering at the University of Edinburgh for the period 1894–97. He was elected a corporate Member of the Institution of Civil Engineers in 1884. He was also a member of the Royal Scottish Society of Arts, the Highland and Agricultural Society and the Royal Meteorological Society. He contributed papers on engineering and scientific subjects to numerous Societies and Congresses, and for one on the building of Dhu Heartach Lighthouse, read before the Institution of Civil Engineers in 1876, he was awarded the Manby Premium. In 1886 he, in conjunction with his brother, revised and edited the 3rd edition of David Stevenson's *Canal and River Engineering*.

He gave evidence on several important engineering matters before Royal Commissions, Parliamentary Committees, and in the Law Courts, and took part in various investigations in connection with optical and acoustical problems.

On Mr Stevenson's retirement on March 31, 1938, the Commissioners of Northern Lighthouses put on record their appreciation of the invaluable services rendered by him during his long term of office as their Engineer, and the Trinity House, London, wrote expressing their thanks for his ready help and co-operation in solving the many lighthouse problems which had arisen in his day, and congratulated him on the advances he made and helped to make in lighthouse technique. A letter of appreciation was also received by him from the Board of Trade.

For fifty-four years he was a Director of the Scottish Equitable Life Assurance Society. A keen golfer, he was a member of several golf clubs, including the "Honourable Company of Edinburgh Golfers," the "Royal and Ancient," and the "New Club," North Berwick, of which last he was Captain for a period of three years. He was also a Member of the Royal Company of Archers, having joined in 1876, and was present on many of the occasions when they acted as Bodyguard in Scotland to Queen Victoria, King Edward VII, and King George V.

In 1882 he married a daughter of the late Mr William Roberts of Beckenham, a cousin of Lord Roberts.

He died at his residence "Troqueer," Kingsknowe, Edinburgh, on April 11, 1938, and is survived by his wife and two daughters, Mrs Peploe (D. E. Stevenson) and Mrs Chambers. During the last year of his life he had been in indifferent health, but only became confined to his room a few days after his retirement from business. Mr Stevenson was held in high respect by all with whom he had business relations.

He was elected a Fellow of the Society in 1884 and served on the Council from 1928–31.

J. D. G.

John Edward Touche, M.I.Mech.E.

JOHN EDWARD TOUCHE was born in 1855. He was the son of an Edinburgh banker, and was the grandson and great-grandson of the Scottish manse. He served the usual apprenticeship as a mechanical engineer with a Leith firm, thereafter practically all his professional career was spent abroad, at first in Australia and New Zealand, but later in the United States of America, he being for twenty-five years connected with the Otis Steel Company of Cleveland, Ohio.

Mr Touche had a highly successful career as a mechanical engineer, and was a Member of the Institution of Mechanical Engineers. Eventually he was able to retire from the active pursuits of his profession and settle in his native city and devote himself to other interests which had occupied his spare time while he was still actively engaged in important engineering projects. He was particularly interested in geographical problems and especially in maps and their production. Through his generosity in providing the necessary funds, the Royal Scottish Geographical Society was able to publish on an extensive scale in 1934—the year of the Society's jubilee—*The Early Maps of Scotland*, a very important piece of work and of great value to Scottish geographical records.

Mr Touche had travelled widely, and his long residence in the United States of America had given him an exceptionally intimate knowledge of the development of engineering in all its branches in that country. He maintained a deep interest until his death in modern methods of the manufacture of steel alloys. He was a man with wide interests, and always took an active share in the scientific and religious life of Edinburgh. He was extremely generous and gave freely from the fortune which he had accumulated by his hard work in his earlier years to any good cause brought to his notice. He was a man of great kindliness of character, with all the old-fashioned courtesy so characteristic of the period of his active career. He was elected a Fellow of the Society in 1935. He died on June 9, 1938, at his residence in Blackford Road, Edinburgh.

T. H. B.

Sir David Percival Dalbreck Wilkie, O.B.E., M.D., Ch.M., F.R.C.S.

SIR DAVID WILKIE was a son of Angus. Fifty-six years ago he was born in Kirriemuir. At the time of his death, although comparatively young in years, he had already established for himself an international reputation as a surgeon, and was recognised as one of the leaders in medicine in this country. A number of factors combined to bring this about: he possessed a personality endowed with an unconscious charm, so that anyone who once came under its sway became thereafter a willing recruit in his service. This charm was enhanced by a voice that when used in private conversation, in the lecture theatre, or through the microphone over the wireless was always a pleasure to listen to, and carried the stamp of simple sincerity and sound conviction.

His school days were spent at the Edinburgh Academy, after which he became a student of medicine of Edinburgh University. He graduated in 1904, and although his record was creditable, it did not so far reveal promise of that brilliancy that later years brought forth.

Wilkie took naturally to surgery as his life's work, drawn to it as work where heroic remedies were used that required delicacy of judgment and delicacy of touch to restore the patient to health again.

Professor F. M. Caird and Sir Harold Stiles found in him an apt pupil and set his feet firmly on the ladder of success. The many practical problems revealed at the bedside, in the wards, and in the operating theatre, which dealt with the comfort, the speed of cure, or even the life of the patient that called for a solution, at once raised in Wilkie the devoted spirit of the research scholar, and to find an answer to these he enrolled as a worker in the Royal College of Physicians' Laboratory. The cause of appendicitis was investigated, as also were the prevention and cure of peritonitis, and that deadly disease, acute intestinal obstruction, he studied by experimental research. The brilliancy with which these problems were investigated, the lucid and accurate way in which the results were set forth, at once drew the attention of the medical world to the fact that again in the Edinburgh Medical School another lamp was lit, another star had risen.

It was now but a short step to England, France, and the continent of North America.

Already a Fellow of the Royal College of Surgeons of Edinburgh, he now became a Fellow of the Royal College of Surgeons of England. He was appointed a corresponding member of the French Academy of Surgery, and on one of his visits to America he was elected an Honorary Fellow of the American College of Surgeons, and delivered the Annual Murphy Oration to the Fellows of that college.

In 1924 he succeeded Alexis Thomson as Professor of Surgery in the University of Edinburgh, when, following his natural inclination, he at once founded the Research Laboratory attached to that department. To these laboratories there were attracted many young research workers from home and abroad.

On shoulders broad and willing, but never very robust, there was now placed a steadily increasing burden: the claims of a systematic chair, the direction of a research department, the duties of a clinical charge, and a most exacting private practice occupied fully his entire working day. To these there were added claims from London, when he was called upon to serve as a member of the Medical Research Council, on the Advisory Board of the Army Medical Staff, and the Scientific Advisory Committee of the British Empire Cancer Campaign. These appointments necessitated frequent journeys to London, and, in addition, he was called upon to address many medical meetings in the provinces.

Perhaps it was the discipline of the navy that Wilkie acquired when serving during the War as a Surgeon Commander in the Royal Naval Volunteer Reserve that led to his ready acceptance of these many calls on his time, or possibly his inability to refuse requests for help that explained his assumption of this staggering load. Under its weight more than once he broke down, but quickly recovered after a short rest, but at last the dread ailment, in the cure of which he had given a life's study, seized him, and after a gallant and courageous effort he finally acknowledged defeat:

"Under the wide and starry sky,
Dig the grave and let me lie.
Glad did I live and gladly die,
And I laid me down with a will.

This be the verse you grave for me:
Here he lies where he longed to be,
Home is the sailor, home from the sea,
And the hunter home from the hill."

He was elected a Fellow of this Society in 1925, and died on August 28, 1938.

H. W.

MALCOLM JAMES ROWLEY DUNSTAN, O.B.E., M.A., late Professor of Agriculture, University of Bristol, was born on August 19, 1863, and educated at Bedford Grammar School, St Paul's School, and Merton College, Oxford. He was Director of the Midland Agricultural and Dairy Institute (1896–1902); Director of Technical Instruction, Notts County Council (1891–1902); Principal of the South-Eastern Agricultural College, Wye, Kent (1902–1922); and Principal of the Royal Agricultural College, Cirencester (1922–1927).

He was elected a Fellow of this Society in 1892 and died on May 28, 1938.

ROBERT BLACK THOMSON, M.B., Ch.B. (Edin.), formerly Professor of Anatomy, University of Cape Town, was elected a Fellow of this Society in 1912, and contributed a valuable paper to its *Transactions* (1909) on "The Osteology of Antarctic Seals (Scottish National Antarctic Expedition, 1902–1904)."

He died on December 17, 1937, at Aliwal North, Cape Province.

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PROCEEDINGS OF THE STATUTORY GENERAL MEETING

Beginning the 155th Session, 1937–1938.

At the Statutory General Meeting, held in the Society's Rooms, 24 George Street, on Monday, October 25, 1937, at 4.30 P.M.

Professor Sir D'Arcy Wentworth Thompson, President, in the Chair.

The Minutes of the Statutory Meeting held on October 26, 1936, were read, approved, and signed.

The President nominated as Scrutineers, for the election of Office-Bearers and Council, Mr THOMAS ROWATT and Mr W. J. M. MENZIES.

The President, before proceeding to the Ballot, requested the Fellows, subject to their approval, to substitute the name of Dr G. W. TYRRELL on the Balloting List for that of Principal O. CHARNOCK BRADLEY, who had withdrawn his name.

The Ballot was then taken.

The General Secretary submitted the following report:—

GENERAL SECRETARY'S REPORT, OCTOBER 25, 1937.

The following Address was sent to His Majesty King George VI, on His Accession to the Throne:—

TO THE
KING'S MOST EXCELLENT MAJESTY

May it please Your Majesty,

We, the President and Fellows of the Royal Society of Edinburgh, tender to Your Majesty our loyal devotion to the Throne.

We recall with pleasure that Your Majesty as Duke of York accepted the Honorary Fellowship of our Society, and we express our gratitude that Your Majesty has been graciously pleased to continue the Sovereign's Patronage of the Society.

We earnestly hope that Your Majesty may long be spared to rule over a peaceful, prosperous, and happy nation, and that every blessing may attend Your Majesty, Her Majesty the Queen, and the Royal Princesses.

(*Signed*) D'ARCY W. THOMPSON, *President*.
JAMES KENDALL, *Secretary*.

January 1937.

An acknowledgment of the Address was received from the Secretary of State for Scotland.

The Society was represented at the Proclamation of His Majesty King George VI, at the Market Cross of Edinburgh, on December 14, 1936, by Lt.-Col. A. G. MCKENDRICK, Dr JAMES WATT, Dr A. C. AITKEN, and Professor JAMES KENDALL.

The President represented the Society at the Coronation of Their Majesties in Westminster Abbey on Wednesday, May 12, 1937.

The Society was also represented at the Coronation Service in St Giles' Cathedral on that day.

A communication was received from the Keeper of the Privy Purse stating that "His Majesty is pleased to intimate to those Societies and Institutions which were recently granted Patronage by King Edward VIII, that they may continue to show the Sovereign as their Patron during His Reign."

His Majesty was graciously pleased to sign the Roll of Fellows as an Honorary Fellow (Elected March 5, 1934), and as the Patron of the Society, on July 7, 1937, when His Majesty was in residence at the Palace of Holyroodhouse.

During the session three Addresses have been given by request of the Council: on January 11, 1937, by Dr F. FRASER DARLING, on "Observations on Animal Sociality"; on February 1, 1937, by Professor JAMES KENDALL, on "Ions and Isotopes"; and on June 7, 1937, in terms of the BRUCE-PRELLER LECTURE FUND, by Professor H. S. TAYLOR, on "Heavy Hydrogen in Scientific Research." On July 5, 1937, Professor C. G. DARWIN opened a discussion on "The

Origin of the Laws of Nature," which was taken part in by Professor W. H. McCREA, Professor E. T. WHITTAKER, Professor MAX BORN, and Mr W. A. SINCLAIR, Department of Philosophy, University of Edinburgh. Professor KENDALL'S Address was published in the *Proceedings* of the Society, vol. 57, 1937, pp. 182–193.

33 papers were read, as compared with 21 in the previous session. The papers were in the following subjects: Mathematics, 8; Physics, 2; Geology, 2; Palæontology, 2; Botany, 4; Zoology, 8; Animal Genetics, 6; and Anatomy, 1. 24 papers have been published in the *Proceedings* and 8 in the *Transactions*. 7 papers have been withdrawn, and several papers are still under the consideration of the Council.

The Society has lost by death 24 Fellows and 6 Honorary Fellows. 40 Fellows and 3 Foreign and 2 British Honorary Fellows were elected.

Invitations were received and the Society was or will be represented as follows on the occasions mentioned:—

1. Centenary of the Army Medical Library, Washington, November 16, 1936. Lt.-Col. EDGAR ERSKINE HUME.
2. 150th Anniversary of the College of Physicians of Philadelphia, May 14, 1937. Letter sent.
3. Lord High Commissioner's Levee at the Palace of Holyroodhouse, May 19, 1937. Three Vice-Presidents and three Members of Council.
4. 250th Anniversary of the Foundation of the K. Leopold Carolinisch d. Deutsche Akademie d. Naturforscher, Halle a Saale, May 28–29, 1937. Letter sent.
5. Inauguration of the Pontifical Academy of Sciences, Citta Vaticana, May 31, 1937. Engrossed letter sent.
6. 23rd Annual Conference of the National Association for the Prevention of Tuberculosis, Bristol, July 1–3, 1937. Professor Sir ROBERT PHILIP.
7. Jubilee of the Buchan Club, Peterhead, August 7, 1937. Professor JAMES RITCHIE and Dr A. BREMNER.
8. Congrès Mondial de la Documentation Universelle, Paris. Août 16–21, 1937. Professor M. CAULLERY was asked, but could not be present. A letter was sent.
9. International Congress of Geology (XVII) Session, Moscow, July to September 1937. Dr G. W. TYRRELL.
10. 150th Anniversary of the Birth of J. E. PURKYNE, Prague, September 24–28, 1937: Letter sent.
11. Réunion Internationale de Physique de Chemie et Biologie. Paris, September 30 to October 7, 1937. Professor MARCELLIN BOULE, Hon. F.R.S.E.
12. 200th Anniversary of the Birth of LUIGI GALVANI, University and City of Bologna, October 1937. President attended and presented an Address.
13. Semi-Jubilee of the Edinburgh Workers' Educational Association at Newbattle Abbey College, October 23, 1937. Dr J. DONALD POLLOCK.
14. International Congress of Geography, Amsterdam, July 18–28, 1938. Professor ALAN G. OGILVIE.

The undernoted were appointed by the Council to fill vacancies in the Society's representation on the following British National Committees:—

Astronomy . . .	Sir FRANK DYSON.
Biology . . .	Professor J. RITCHIE.
Geodesy and Geophysics	Sir JOHN FLETT.
Geography . . .	Mr J. BARTHOLOMEW.
Physics . . .	Professor J. A. CARROLL.
Scientific Radio . .	Emeritus Professor C. T. R. WILSON.

Dr A. CRICHTON MITCHELL was re-appointed to serve as the Society's representative on the Governing Body of the Heriot-Watt College for three years as from January 1, 1937.

Dr L. DOBBIN represented the Society at a Conference in the Rooms of the Royal Society of London, on December 15, 1936, to discuss the question of a Standard System of Bibliographical References and Abbreviations to be used in Scientific Publications.

Professor F. A. E. CREW was appointed by the Council to succeed the late Professor D. F. FRASER-HARRIS as the representative of the Society on the Leonard Darwin Studentship Committee of the Eugenics Society, London.

Professor T. J. MACKIE was reappointed as the joint representative of the University of Edinburgh and the Society on the India Office Consultative Committee to assist in questions connected with the recruitment of medical research workers for service in India, for three years, as from February 24, 1936.

Professor J. WALTON was appointed as the Society's representative on the Scientific and Technical Committee of the Empire Exhibition, Scotland, 1938.

Dr A. LANDSBOROUGH-THOMSON was appointed to act as a representative of the Society, with Professor James Ritchie, on the British Section of the International Committee for the Preservation of Birds, in succession to Professor J. Graham Kerr, who resigned.

Dr D. A. Bannerman (British Museum, Natural History), through our representatives, was appointed to represent the Society at the meeting of the European Continental Section of the International Committee for the Preservation of Birds, in Vienna, from July 3 to 6, 1937.

A Committee was appointed to make arrangements jointly with the Edinburgh Mathematical Society for the Celebration of the Tercentenary of James Gregory in July 1938.

During the session the sum of £300 was expended on the binding of books in the Library. Arrears of binding are being gradually overtaken.

The oil portraits in the possession of the Society have been cleaned and renovated by an expert under the eye of Mr Stanley Cursiter, O.B.E., R.S.A., Director of the National Galleries of Scotland.

The GUNNING VICTORIA JUBILEE PRIZE (1932–1936) was presented to Professor C. G. Darwin, Master of Christ's College, Cambridge, and formerly Tait Professor of Natural Philosophy in the University of Edinburgh, for his distinguished contributions in mathematical physics; and the MAKDOUGALL-BRISBANE PRIZE (1934–1936) to Dr E. M. Anderson, formerly of H.M. Geological Survey (Scotland), for his paper on "The Dynamics of the Formation of Cone-sheets, Ring-dykes, and Caldron-subsidences," published in the Society's *Proceedings* within the period of the award.

The acknowledgments of the Society are due to the Carnegie Trust for the Universities of Scotland for grants to authors towards the cost of illustrations, tabular matter, etc., of papers published in the *Transactions* and *Proceedings*, amounting to £133, 9s. 11d.; to Queen's University, Belfast, for a grant of £15 towards the publication of Professor J. Small's joint paper in the *Proceedings*; to Birkbeck College, London, for £5 towards the cost of the illustrations of Dr Vera Fretter's paper in the *Transactions*; and for £300 received from the Royal Society of London, from the Government Publication Grant, in aid of the cost of the Society's publications for the session 1936–1937.

Treasurer's Report:—

The Treasurer, in submitting the Accounts for the past year, mentioned briefly the leading items of Receipts and Expenditure and compared them with those of the previous year. He stated that a sum of £200, set aside in the Accounts for the session 1934–35, had now been absorbed. He indicated that the financial position of the Society was satisfactory.

Dr R. A. Fleming moved the adoption of the reports, and the reappointment of Messrs Lindsay, Jamieson & Haldane, C.A., as auditors for the ensuing session. The meeting approved.

The Scrutineers reported that the Ballot Papers were in order, and the President declared that the following Office-Bearers and Members of Council had been duly elected:—

Professor Sir D'Arcy W. Thompson, Kt., C.B., D.Litt., Hon. D.Sc., LL.D., F.R.S., President.
Professor F. A. E. Crew, M.D., D.Sc., Ph.D.
Lt.-Col. A. G. McKendrick, M.B., D.Sc., F.R.C.P.E.
Principal J. C. Smail, O.B.E., Companion Inst.E.E.
Professor J. Walton, M.A., D.Sc.
James Watt, W.S., LL.D.
Professor E. T. Whittaker, M.A., Hon. Sc.D., LL.D., F.R.S.
} Vice-Presidents.
Professor James P. Kendall, M.A., D.Sc., F.R.S., General Secretary.
Alexander C. Aitken, M.A., D.Sc., F.R.S.
Charles H. O'Donoghue, D.Sc.
} Secretaries to Ordinary Meetings.
E. Maclagan Wedderburn, O.B.E., D.K.S., M.A., D.Sc., Treasurer.
Leonard Dobbin, Ph.D., Curator of Library and Museum.

MEMBERS OF COUNCIL.

Edwin Bramwell, M.D., LL.D., F.R.C.P. Lond. and Edin.
Emeritus Professor T. H. Bryce, M.A., M.D., LL.D., F.R.S.
Professor I. de Burgh Daly, M.A., M.D., B.Ch.
John Alexander Inglis, K.C., M.A., LL.B.
Professor A. D. Peacock, D.Sc.
John E. Mackenzie, D.Sc.
Professor Sydney Smith, M.D., F.R.C.P., D.P.H.
Emeritus Professor Ralph Stockman, M.D., LL.D., F.R.C.P.E.
Professor Lancelot T. Hogben, M.A., D.Sc., F.R.S.
Professor James Ritchie, M.A., D.Sc.
G. W. Tyrrell, A.R.C.S., D.Sc., F.G.S.
Emeritus Professor C. T. R. Wilson, C.H., M.A., D.Sc., LL.D., F.R.S.

The Scrutineers were thanked for their services.

The PRESIDENT paid a tribute to the valuable services rendered to the Society by Dr JAMES WATT, who had retired by rotation after eleven years service as Treasurer, and who that day had been elected a Vice-President.

The retiring Office-Bearers and Members of Council were also warmly thanked for their services.

The PRESIDENT, Emeritus Professor C. T. R. WILSON, and Professor MAX BORN spoke in high appreciation of the scientific achievements of the late Lord Rutherford of Nelson, and expressed the Society's sorrow at his untimely death. It was agreed that a minute of appreciation and condolence should be sent by the Council to Lady Rutherford.

In presenting the BRUCE PRIZE (1936) to Mr JAMES WILLIAM SLESSER MARR, the PRESIDENT said:—

> A Committee consisting of representatives of the Royal Society of Edinburgh, the Royal Physical Society and the Royal Scottish Geographical Society, has awarded the DR W. S. BRUCE MEMORIAL PRIZE (1936) to Mr JAMES W. S. MARR, M.A., B.Sc., who first went to Polar Regions with Sir Ernest Shackleton in the *Quest* in 1921, sailing as a Boy Scout. On Shackleton's death the Expedition continued under Commander Worsley into the Weddell Sea. MARR next sailed with Commander Worsley in 1925 to Spitsbergen and White Island in the Algarsson Expedition. In 1927 he joined the staff of the R.R.S. *Discovery*; and since then, with brief intervals at home, he has spent his time in the Southern Ocean, partly in the old *Discovery* and partly in *Discovery II*. From 1929 to 1931 he was in *Discovery* when she was lent to Sir Douglas Mawson for the British-Australian-New Zealand Expedition which found many new stretches of the coast-line of Antarctica. In November 1935 MARR published in the "*Discovery*" *Reports* a monograph on the South Orkney Islands, which greatly extended the original researches of Dr W. S. BRUCE on that Antarctic Group. He has recently returned from another Antarctic voyage in *Discovery II*.

The PRESIDENT then called upon Mr MARR to deliver his Address on "Antarctic Surveys: The Work of the 'Discovery' Investigations."

The PRESIDENT, in name of the Society, cordially thanked Mr MARR for his Address.

PROCEEDINGS OF THE ORDINARY MEETINGS,
Session 1937–38.

FIRST ORDINARY MEETING.

Monday, November 8, 1937.

Sir D'Arcy Wentworth Thompson, President, in the Chair.

The Minutes of the previous Ordinary Meeting were taken as read, and signed.

The General Secretary read a minute of appreciation of the late Rt. Hon. LORD RUTHERFORD of Nelson.

The following Communications were submitted:—

1. The Sex Ratio of the Domestic Fowl and its bearing upon the Sex Linked Lethal Theory of Differential Mortality. By Professor F. A. E. CREW, M.D., D.Sc. *Proc.*, vol. 58, pp. 73–79.
2. Factors affecting the Hatching Weight of Brown Leghorn Chickens. By Miss NANCY GALPIN, M.Sc., D.Sc. Communicated by Dr A. W. GREENWOOD. *Proc.*, vol. 58, pp. 98–113.
3. Gynandromorphism and Lateral Asymmetry in Birds. By Professor F. A. E. CREW, M.D., D.Sc., and Mr S. S. MUNRO, B.S.A., M.S. *Proc.*, vol. 58, pp. 114–134.

SECOND ORDINARY MEETING.

Monday, December 6, 1937.

Sir D'Arcy Wentworth Thompson, President, in the Chair.

The Minutes of the previous Ordinary Meeting were taken as read, and signed.

At the request of the Council an address was delivered by Dr H. J. BHABHA on "The Production of Electron Showers by Cosmic Rays."

The following Communications were submitted:—

1. The Decline of the Birth-rate: Regularities revealed by an Analysis of the Rates observed in certain European Countries. By R. S. BARCLAY, B.Sc., and W. O. KERMACK, D.Sc., LL.D. *Proc.*, vol. 58, pp. 55–72.

Read by Title:—

2. Quantitative Evolution: IV.—Deductions from the BAT Curve. V.—The Free and Apparent Dp-ages of Compositæ. VI.—Further Deductions from the BAT Curve. By Professor J. SMALL, D.Sc. *Proc.*, vol. 58, pp. 14–54.
3. Induction Proofs of the Relations between certain Asymptotic Expansions and Corresponding Generalised Hypergeometric Functions. By Professor T. M. MACROBERT, D.Sc. *Proc.*, vol. 58, pp. 1–13.

THIRD ORDINARY MEETING.

Monday, January 10, 1938.

Sir D'Arcy Wentworth Thompson, President, in the Chair.

The Minutes of the previous Ordinary Meeting were taken as read, and signed.

The following Communications were submitted:—

1. The Hairs of the Monotremata, with special reference to their Cuticular Scale Pattern. By A. B. Wildman and S. Manby. Communicated by Professor J. Ritchie, D.Sc. *Trans.*, vol. 59, pp. 333–349.

2. The Structure and Function of the Alimentary Canal of Æolid Molluscs, with a Discussion on their Nematocysts. By A. Graham, M.A., B.Sc. Communicated by Dr C. H. O'Donoghue. *Trans.*, vol. 59, pp. 267–307.

3. On some Undescribed Species from the Lower Carboniferous Flora of Berwickshire; together with a Note on the Genus *Stenomyelon* Kidston. By Mary G. Calder, B.Sc., Ph.D. Communicated by Professor J. Walton, D.Sc. *Trans.*, vol. 59, pp. 309–331.

Read by Title:—

4. Studies on Reproduction in the Albino Mouse. I.—The Period of Gestation and the Time of Parturition. By Professor Hugo Merton. Communicated by Professor F. A. E. Crew, M.D., D.Sc. *Proc.*, vol. 58, pp. 80–97.

FOURTH ORDINARY MEETING.

Monday, February 7, 1938.

Sir D'Arcy Wentworth Thompson, President, in the Chair.

The Minutes of the previous Ordinary Meeting were taken as read, and signed.

At the request of the Council Dr G. W. Tyrrell, A.R.C.Sc., F.G.S., delivered an address on "Geology in the U.S.S.R." (an account of the Seventeenth International Geological Congress, Moscow, 1937, and of Excursions to Karelia, Kola, and Siberia).

FIFTH ORDINARY MEETING.

Monday, March 7, 1938.

Sir D'Arcy Wentworth Thompson, President, in the Chair.

The Minutes of the previous Ordinary Meeting were taken as read, and signed.

The Ballot for the election of Ordinary Fellows then took place. The President nominated Mr R. T. Skinner and Professor W. T. Gordon as Scrutineers. The following gentlemen were declared duly elected:—

Charles Henry William Gatacre Anderson, Paul Bacsich, David Armitage Bannerman, Alexander William Morton Beveridge, Geoffrey Bernard Brook, Charles Augustus Carlow, Sir Iain Colquhoun, Martin Melvin Cruickshank, Stanley Cursiter, John Michael Dewar, Norman McOmish Dott, The Rt. Hon. Lord Elphinstone, Charles Henry Pearson Gifford, Cecil Gordon, William Smith Gordon, Ram Kumar Goyal, James Robertson Campbell Greenlees, George Hogarth, James Dalgleish Hamilton Jamieson, Allister Middleton MacGillivray, Alexander Mackie, William Hutchison McMillan, Donald Mainland, Charles Alexander Malcolm, Sir John Maxwell Stirling Maxwell, Harry Henderson Monteath, Sanford Sterling Munro, Thomas Crawford Phemister, Andrew Maitland Ramsay, The Rt. Hon. The Earl of Rosebery, James Sandilands, Arthur Henry Havens Sinclair, James Stewart, John Livingstone Stewart, Arthur Landsborough Thomson, Robert Thomson, Andrew Topping, Arthur Elijah Trueman, Oswald James Walker, Robert Wilson, George McCreath Wyburn.

The President announced that the KEITH PRIZE for the period 1935 to 1937 had been awarded to Professor HAROLD STANLEY RUSE, M.A., for his paper "On the Geometry of Dirac's Equations and their Expression in Tensor Form," published in the *Proceedings* of the Society within the period, and for his other papers in the *Proceedings*.

The following Communications were submitted:—

1. On *Tetrastichia bupatides*, a Carboniferous Pteridosperm from East Lothian. By Professor W. T. Gordon, M.A., D.Sc. *Trans.*, vol. 59, pp. 351–370.

2. An Analysis and Comparison of the Structural Features of *Dactylotheca plumosa* Artis and *Senftenbergia ophiodermatica* Göpp. By Norman W. Radforth, M.A. (Toronto). Communicated by Professor J. Walton, M.A., D.Sc. *Trans.*, vol. 59, pp. 385–396.

Read by Title:—

3. Studies in Practical Mathematics. III.—The Application of Quadratic Extrapolation to the Evaluation of Derivatives, and to Inverse Interpolation. By A. C. Aitken, M.A., D.Sc., F.R.S. *Proc.*, vol. 58, pp. 161–175.

SIXTH ORDINARY MEETING.

Monday, May 2, 1938.

Sir D'Arcy Wentworth Thompson, President, in the Chair.

The Minutes of the previous Ordinary Meeting were taken as read, and signed.

The following signed the Roll and were admitted to Fellowship: Mr Charles Henry Williams Gatacre Anderson, Mr Charles Augustus Carlow, Mr Stanley Cursiter, Dr John Michael Dewar, Mr Norman McOmish Dott, Mr Charles Henry Pearson Gifford, Dr William Smith Gordon, Dr James Robertson Campbell Greenlees, Dr Alexander Mackie, Professor Harry Henderson Monteath, Dr Andrew Maitland Ramsay, Mr James Sandilands, Dr James Stewart, Mr Robert Wilson, Dr Horace George Smith.

The President announced that the following names had been proposed by the Council for Honorary Fellowship:—

British.

Sir Thomas Lewis, C.B.E., F.R.S.
Professor Geoffrey Ingram Taylor, F.R.S.

Foreign.

Professor Federigo Enriques, Rome.
Professor H. N. Russell, For.Mem.R.S., Princeton.
Professor Dr Karl Freiherr von Tubeuf, Munich.

It was intimated that the Council had awarded the NEILL PRIZE for the period 1935 to 1937 to Professor WILLIAM J. HAMILTON, M.D., D.Sc., St Bartholomew's Hospital, for his contributions to the Embryology of the Ferret and other work published in the *Transactions* of the Society.

It was announced that Professor P. A. M. DIRAC, F.R.S., had accepted the invitation of the Council to deliver the JAMES SCOTT LECTURE on a subject dealing with "The Fundamental Concepts of Natural Philosophy" on February 6, 1939.

The following Communications were submitted:—

1. The Life-History and Development of *Agriolimax agrestis* L., the Gray Field Slug. By Robert Carrick, B.Sc., Ph.D. Communicated by Dr A. E. Cameron. *Trans.*, vol. 59, pp. 563–597.

2. The Brackish-water Lochs of Orkney. By Edith A. T. Nicol, B.A., Ph.D. Communicated by the President. *Proc.*, vol. 58, pp. 181–191.

3. An Investigation of the Mucorales in the Soil. By Marie E. Campbell, B.Sc., Ph.D. Communicated by Dr Malcolm Wilson. *Trans.*, vol. 59, pp. 411–436.

Read by Title:—

[illegible] Green's Function for an Ellipse, and its Application to the Motion of a Point Vortex. By D. Meksyn, D.Sc. Communicated by Professor E. T. Whittaker, F.R.S. *Proc.*, vol. 58, pp. 176–180.

SEVENTH ORDINARY MEETING.

Monday, June 6, 1938.

Sir D'Arcy Wentworth Thompson, President, in the Chair.

The Minutes of the previous Ordinary Meeting were taken as read, and signed.

The following signed the Roll and were admitted to Fellowship: Dr GEOFFREY BERNARD BROOK, Mr JAMES DALGLEISH HAMILTON JAMIESON, Dr ALLISTER MACGILLIVRAY, Dr JOHN MCMICHAEL, Dr ARTHUR HENRY HAVENS SINCLAIR, Dr ROBERT THOMSON, and Dr CHARLES ALEXANDER MALCOLM.

The following Communications were submitted:—

1. Differential Fertility in Scotland, 1911–1931. Part I. By ENID CHARLES, M.A., Ph.D. Communicated by Professor LANCELOT HOGBEN, F.R.S. *Trans.*, vol. 59, pp. 371–383.

2. The Food and Feeding of the Brown Trout (*Salmo trutta* Linné) in relation to the Organic Environment. By R. M. NEILL, M.C., M.A. Communicated by Professor LANCELOT HOGBEN, F.R.S. *Trans.*, vol. 59, pp. 481–520.

3. Malformations in the Adult Salmon as a Key to the Understanding of the Fate of Smolts during their Sojourn in the Sea. By Professor V. TCHERNAVIN. Communicated by Professor JAMES RITCHIE, D.Sc. *Proc.*, vol. 58, pp. 233–241.

Read by Title:—

4. The Actinopterygian Fishes from the Lower Carboniferous of Glencartholm, Eskdale, Dumfriesshire. By J. A. MOY-THOMAS, M.A., and Miss BRADLEY DYNE, B.A. Communicated by Dr A. C. STEPHEN. *Trans.*, vol. 59, pp. 437–480.

5. The Dynamics of Sheet Intrusion with some Considerations on Faulting. By E. M. ANDERSON, M.A., D.Sc., F.G.S. *Proc.*, vol. 58, pp. 242–251.

6. On Rare Defects in Human Populations with particular regard to In-Breeding and Isolate Effects. By Professor GUNNAR DAHLBERG, M.D., LL.D. Communicated by Professor F. A. E. CREW, M.D., D.Sc. *Proc.*, vol. 58, pp. 213–232.

EIGHTH AND LAST ORDINARY MEETING.

Monday, July 4, 1938.

Sir D'Arcy Wentworth Thompson, President, in the Chair.

The Minutes of the previous Ordinary Meeting were taken as read, and signed.

Dr GEORGE GREEN and Mr GEOFFREY B. BROOK signed the Roll and were admitted to Fellowship.

JAMES GREGORY TERCENTENARY.

The members of the ST ANDREWS MATHEMATICAL COLLOQUIUM (July 4 to 15, 1938) attended the Meeting by the cordial invitation of the Society.

The following Papers were submitted from 3 to 4 p.m.

1. James Gregory, and his Unpublished Discoveries. By Professor H. W. TURNBULL, F.R.S. *Gregory Memorial Volume.*

2. On James Gregory's *Geometriæ Pars Universalis*. By Dr ADOLF PRAG. *Gregory Memorial Volume.*

Read by Title:—

3. Piccole note su James Gregory e il suo soggiorno in Italia. By Professor FEDERIGO ENRIQUES, Rome. *Gregory Memorial Volume.*

4. On James Gregory's *Vera Quadratura*. By Professors M. DEHN and E. HELLINGER, Frankfort a.M. *Gregory Memorial Volume.*

After a few remarks by the President the Meeting adjourned for tea until 4·30.

The following, proposed by the Council for Honorary Fellowship, were unanimously elected:—

FOREIGN HONORARY FELLOWS.

FEDERIGO ENRIQUES, Rome.
HENRY NORRIS RUSSELL, Princeton.
KARL FREIHERR VON TUBEUF, Munich.

BRITISH HONORARY FELLOWS.

Sir THOMAS LEWIS, C.B.E., F.R.S., London.
GEOFFREY INGRAM TAYLOR, F.R.S., Cambridge.

The President thanked the appointed Scrutineers—Mr T. H. GILLESPIE and Mr J. W. BUTTERS.

The Visitors were admitted and the KEITH and NEILL PRIZES presented:—

Presentation of the KEITH PRIZE (1935–1937) to Professor HAROLD STANLEY RUSE, M.A.

When in 1928 Dirac published the set of partial differential equations named after him, he removed from Quantum Mechanics one point of discordance with the Special Theory of Relativity, but at the same time introduced an apparent disagreement with the General Theory; the new equations did not obey the tensor-laws of transformation which are postulated by the latter theory for all physically significant formulæ, and, as Darwin wrote at the time, it was rather disconcerting to find that apparently something had escaped through the net. In the following year van der Waerden began the work of closing the net by introducing into special-relativity Quantum Mechanics a new kind of mathematical entity, the two-component spinor, and later writers described his work in geometrical terms and formalised it in such a way as to make possible its extension to General Relativity. The full story of the two-component spinor was not, however, told until Professor Ruse wrote the paper for which the present award is principally being made. Recognising the geometrical significance of investigations into the relations between the Tensor Calculus and Spinor Calculus, he wrote a full account of the theory of two-component spinors which co-ordinated the work of previous writers and developed the geometrical description of the Dirac Theory, in a simple and original fashion, to a point considerably beyond that reached by other investigators. The paper has gained considerable attention abroad, and remains the most complete account of the theory of two-component spinors yet written. Taken in conjunction with earlier papers on Relativity, published in the *Proceedings* of this Society and elsewhere, it establishes Professor Ruse's reputation as an expert on the mathematics of Relativity and kindred theories.

Presentation of NEILL PRIZE (1935–1937) to Professor WILLIAM J. HAMILTON, M.D., D.Sc.

With the investigation of the presomite stages of mammalian development are associated some of the greatest names among Embryologists. That of Bonnet is honourably connected with the study of these stages in Carnivores. His intensive and comprehensive papers on the development of the dog are very well known. The corresponding stages in the ferret were studied by Professor Arthur Robinson—but no systematic account existed of the details until the appearance of Professor Hamilton's papers. They therefore broken ew ground, and will have a permanent and honourable place in the literature of the subject. They are noteworthy for the completeness of the record up to the formation of the mesoderm, and for the excellence of the technique they display. The account of the segmentation of the egg and of the formation of the blastocyst is enriched and enlightened by excellent photomicrographs of the living egg, the obtaining of which involved much skill and patience. The demonstration provided of the irregularity of segmentation in mammals is convincingly demonstrated. In the later phases perhaps the most noteworthy points are the demonstration of the existence of a prochordal process and the very competent analysis of the early phases of the mesoblast.

The careful comparison with the stages in other mammals; the capable discussion of the theoretical implications of the processes in ferret; and the excellence of the illustrations make the work well worthy of the recognition of the Society as an outstanding piece of original research—and a valuable contribution to embryological literature.

The President intimated that the Joint-Committee of representatives of the Royal Society of Edinburgh, the Royal Physical Society, and the Royal Scottish Geographical Society had awarded the DR W. S. BRUCE MEMORIAL PRIZE (1938) to Mr ALEXANDER R. GLEN for his work in Spitsbergen, including survey in New Friesland and the completion of the map of North East Land, and that the Prize would be presented at a later Meeting.

He also intimated that the DAVID ANDERSON-BERRY PRIZE (1938) had been awarded to Miss MARY A. C. COWELL, M.B., Holt Radium Institute, Manchester, for her Essay entitled "An Investigation into Some of the Factors affecting the Response of Human Skin and Human Skin Tumours to Radiation."

The Society was presented with a portrait of the President, painted by Mr DAVID S. EWART, A.R.S.A. Professor F. A. E. CREW, Vice-President, made the presentation on behalf of the subscribers. The PRESIDENT expressed his thanks for the tribute paid to him, and the Artist also expressed his thanks for the way in which his work had been received.

The following Papers were read by Title:—

1. Note sur les Crinoïdes de la "Scotia." By Professor C. VANEY. Communicated by Dr A. C. STEPHEN.

2. The Association of Non-homologous Chromosomes in Corixidæ (Hemiptera-Heteroptera). By H. D. SLACK, B.Sc. Communicated by Professor F. A. E. CREW, M.D., D.Sc. *Proc.*, vol. 58, pp. 192–212.

3. The Female Reproductive System and Corpora lutea of the False Killer Whale, *Pseudorca crassidens* Owen. By L. C. COMRIE, B.Sc., and ANN B. ADAM, B.Sc. Communicated by Professor A. D. PEACOCK, D.Sc. *Trans.*, vol. 59, pp. 521–531.

4. Factors affecting Postnatal Growth of Brown Leghorn Chickens. By N. GALPIN, D.Sc. Communicated by Dr A. W. GREENWOOD.

5. Studies on Plumage in the Male Brown Leghorn Fowl. By JEN PAO CHU, B.Sc. Communicated by Dr A. W. GREENWOOD. *Trans.*, vol. 59, pp. 533–562.

6. On *Rhamphodopsis*, a Ptyctodont from the Middle Old Red Sandstone of Scotland. By Professor D. M. S. WATSON, F.R.S. Communicated by Dr C. H. O'DONOGHUE. *Trans.*, vol. 59, pp. 397–410.

7. Seasonal Trends of Births in Scotland. By Professor W. P. KENNEDY, Ph.D.

PROCEEDINGS OF THE STATUTORY GENERAL MEETING

Ending the 155th Session, 1937–1938.

At the Statutory General Meeting, held in the Society's Rooms, 24 George Street, on Monday, October 24, 1938, at 4.30 P.M.

Sir D'Arcy Wentworth Thompson, President, in the Chair.

The Minutes of the Statutory Meeting held on October 25, 1937, were read, approved, and signed.

The President nominated as Scrutineers, for the election of Office-Bearers and Council, Mr WILLIAM FRASER and Mr F. C. MEARS.

The Ballot was then taken.

The General Secretary submitted the following report:—

GENERAL SECRETARY'S REPORT, OCTOBER 24, 1938.

During the session three Addresses have been given by request of the Council: on October 25, 1937, by Mr J. W. SLESSER MARR, on "Antarctic Surveys: the Work of the 'Discovery' Investigations"; on December 6, 1937, by Dr H. J. Bhabha, on "The Production of Electron Showers by Cosmic Rays"; and on February 7, 1938, by Dr G. W. TYRRELL, on "Geology in the U.S.S.R." On July 4, 1938, the Society celebrated, conjointly, with the members of the ST ANDREWS MATHEMATICAL COLLOQUIUM (July 4 to 15, 1938), the Tercentenary of the birth of JAMES GREGORY, the Scottish Mathematician. Certain papers on his life and work were read which will be published by the Society in a GREGORY MEMORIAL VOLUME, edited by Professor H. W. TURNBULL, F.R.S., and Dr A. C. AITKEN, F.R.S.

37 papers were read as compared with 33 in the previous session. The papers were on the following subjects: Mathematics and Statistics, 6; JAMES GREGORY papers, 5; Geology and Palæontology, 6; Botany, 4; Zoology, 8; Animal Genetics, 8. 13 papers have been published in the *Transactions* and 16 in the *Proceedings*. 5 papers on the life and work of JAMES GREGORY will be published in the Gregory Memorial Volume. 6 papers have been withdrawn, and several papers are still under the consideration of the Council.

The Society has lost by death 18 Fellows and 3 Honorary Fellows. 41 Fellows and 3 Foreign and 2 British Honorary Fellows were elected. 4 Fellows resigned and 3 Fellows were removed from the Roll.

Invitations were received and the Society was represented as follows on the occasions mentioned:—

1. Jubilee of MAURICE LUGEON, Lausanne, November 20, 1937. Engrossed letter sent.
2. 140th Anniversary of the Naturhistorische Gesellschaft zu Hannover, December 11, 1937. Letter sent.
3. Centenary of the Trevandrum Observatory, India, December 23, 1937. Letter sent.
4. 150th Anniversary of the Royal Botanic Garden, Calcutta, January 6, 1938. Letter sent.
5. 50th Anniversary of the Geographical Society of Finland, Helsingfors, January 22, 1938. Letter sent.
6. International Congress of Leprosy, Cairo, March 21, 1938. Letter sent.
7. Association Guillaume Budé, Strasbourg, April 19–24, 1938. Letter sent.
8. Centenary of the Societas Scientiarum Fennica, April 28–29, 1938. Letter sent.
9. Dedication of the Franklin Institute, Philadelphia, May 19–21, 1938. Principal Sir J. C. IRVINE, F.R.S.
10. 150th Anniversary of the Linnean Society of London, May 24–26, 1938. The PRESIDENT.
11. Lord High Commissioner's Levee at the Palace of Holyroodhouse, May 25, 1938. Professor F. A. E. CREW, Lt.-Col. A. G. MCKENDRICK, Dr JAMES WATT, and Dr C. H. O'DONOGHUE.
12. University of St Andrews, Commemoration of the Tercentenary of the birth of JAMES GREGORY, July 5, 1938. Dr A. C. AITKEN, F.R.S.

13. Congrès Internationale des Sciences Anthropologiques et Ethnographiques, Copenhagen, August 1–6, 1938. Professor V. GORDON CHILDE.
14. International Congress of Entomology, Berlin, August 15–20, 1938. Dr A. E. CAMERON.
15. 14th International Conference of the International Federation for Documentation, Oxford, September 21–26, 1938. Dr DOUGLAS GUTHRIE.
16. Astronomical Society of Edinburgh. Opening of Calton Hill Observatory Buildings, October 7, 1938. The PRESIDENT.

Early in the session a General Committee was formed, consisting of the Council of the Society and a number of leaders in science and education, to secure a portrait of the President—Sir D'ARCY WENTWORTH THOMPSON—to be hung in the Rooms of the Society. Mr DAVID S. EWART, A.R.S.A., was commissioned to paint the portrait. Dr JAMES WATT kindly consented to act as Treasurer of the Fund, and a sum of approximately £370, from which certain expenses fall to be deducted, was contributed by Fellows of the Society and others interested. The portrait was completed, and was presented to the Society, on behalf of the subscribers, by Professor F. A. E. CREW, at the Ordinary Meeting held on July 4, 1938. A smaller portrait will be presented to the President.

An inscription marking the birthplace of JAMES CLERK MAXWELL, Natural Philosopher, has been placed by the Society, with the approval of the Hon. LORD ROBERTSON, the owner, on the house at 14 India Street, Edinburgh. The lettering was designed by Mr L. C. EVETTS, A.R.C.A., King's College, Newcastle-upon-Tyne.

The PRESIDENT was appointed as the representative of the Society on the Meteorological Committee of the Meteorological Office, London.

A dinner was held in the Rooms of the Society on June 23, 1938, in honour of Professor MAX PLANCK, Hon.F.R.S.E., then on a visit to Scotland.

At the Ordinary Meeting on July 4, 1938, the KEITH PRIZE (1935–1937) was presented to Professor HAROLD STANLEY RUSE, M.A., for his paper "On the Geometry of Dirac's Equations and their Expression in Tensor Form," published in the *Proceedings* of the Society within the period, and for his other papers in the *Proceedings*; and the NEILL PRIZE (1935–1937) to Professor WILLIAM J. HAMILTON, M.D., D.Sc., for his contributions to the Embryology of the Ferret and other work published in the *Transactions* of the Society.

The DR W. S. BRUCE MEMORIAL PRIZE (1938) was awarded by the Joint Committee to Mr ALEXANDER R. GLEN, for his work in Spitsbergen, including survey in New Friesland and the completion of the map of North East Land. The Prize will be presented on December 5, 1938.

The JAMES SCOTT LECTURE (1938), on a subject dealing with the fundamental concepts of Natural Philosophy, will be delivered by Professor PAUL ADRIEN MAURICE DIRAC, F.R.S., on February 6, 1939.

The DAVID ANDERSON-BERRY PRIZE (1938) was awarded to MARY A. C. COWELL, M.B., Holt Radium Institute, Manchester, for her essay entitled "An Investigation into some of the Factors affecting the Response of Human Skin and Human Skin Tumours to Radiation." The Prize will be presented on December 5, 1938.

The sum of £300 was expended on Library binding during the session. Arrears in this Department are being gradually overtaken.

The thanks of the Society are due to those who have made presentations to the Library. These include a valuable collection of old biological volumes presented by Mr WILLIAM WILLIAMSON, a Fellow of the Society.

The acknowledgments of the Society are due to the Carnegie Trust for the Universities of Scotland for grants to authors towards the cost of illustrations, tabular matter, etc., of papers published in the *Transactions* and *Proceedings*, amounting to £203, 19s. 3d.; to Birkbeck College Publications Fund for a grant of £10 towards the publication of Mr A. GRAHAM'S paper in *Transactions* (1938); to Professor W. T. GORDON, D.Sc., for £20 towards the plates of his paper in *Transactions* (1938); and for £300 received from the Royal Society of London, from the Government Publication Grant, in aid of the cost of the Society's publications for the session 1937–1938.

TREASURER'S REPORT:—

The TREASURER, in submitting the Accounts for the past year in a new form, mentioned the leading items of Receipts and Expenditure and compared them with those of the previous year. He stated that a sum of £200 had been set aside in the Accounts towards the cost of printing the GREGORY MEMORIAL VOLUME, and indicated that the financial position of the Society was satisfactory.

The Rt. Hon. LORD SALVESEN moved the adoption of the reports, and the reappointment of Messrs LINDSAY, JAMIESON & HALDANE, C.A., as auditors for the ensuing session. The meeting approved.

The Scrutineers reported that the Ballot Papers were in order, and the President declared that the following Office-Bearers and Members of Council had been duly elected:—

Sir D'Arcy W. Thompson, Kt., C.B., D.Litt., Hon. D.Sc., LL.D., F.R.S., President.
Professor F. A. E. Crew, M.D., D.Sc., Ph.D.
Lt.-Col. A. G. McKendrick, M.B., D.Sc., F.R.C.P.E.
Principal J. C. Smail, O.B.E., Companion Inst.E.E.
Professor J. Walton, M.A., D.Sc.
James Watt, W.S., LL.D.
Professor E. T. Whittaker, M.A., Hon.Sc.D., LL.D., F.R.S.
} Vice-Presidents.
Professor James P. Kendall, M.A., D.Sc., F.R.S., General Secretary.
Alexander C. Aitken, M.A., D.Sc., F.R.S.
Charles H. O'Donoghue, D.Sc.
} Secretaries to Ordinary Meetings.
E. Maclagan Wedderburn, O.B.E., LL.D., D.K.S., Treasurer.
Leonard Dobbin, Ph.D., Curator of Library and Museum.

MEMBERS OF COUNCIL.

John E. Mackenzie, D.Sc.
Professor Sydney Smith, M.D., F.R.C.P., D.P.H.
Emeritus Professor Ralph Stockman, M.D., LL.D., F.R.C.P.E.
Professor Lancelot T. Hogben, M.A., D.Sc., F.R.S.
Professor James Ritchie, M.A., D.Sc.
G. W. Tyrrell, A.R.C.S., D.Sc., F.G.S.
Emeritus Professor C. T. R. Wilson, C.H., M.A., D.Sc., LL.D., F.R.S.
Professor R. C. Garry, M.B., Ch.B., D.Sc.
Professor R. J. D. Graham, M.A., D.Sc.
Professor D. Murray Lyon, M.D., F.R.C.P.E., D.P.H., D.Sc.
J. E. Richey, M.C., B.A., Sc.D., F.R.S., F.G.S.
The Hon. Lord Robertson.

The Scrutineers were thanked for their services.

The President thanked the retiring Members of Council for their services.

The President referred to the loss the Society had sustained by the deaths of 18 Ordinary and 3 Honorary Fellows, including several distinguished and old Fellows of the Society.

Visitors having been admitted the President called upon Mr J. L. Baird, Hon.F.R.S.E., to deliver his Address on "The Development of Television."

The President, in name of the Society, cordially thanked Mr Baird for his Address.

THE KEITH, MAKDOUGALL-BRISBANE, NEILL, GUNNING VICTORIA JUBILEE, JAMES SCOTT, BRUCE, AND DAVID ANDERSON-BERRY PRIZES, AND THE BRUCE-PRELLER LECTURE FUND.

The above Prizes will be awarded by the Council in the following manner:—

I. KEITH PRIZE.

The KEITH PRIZE, consisting of a Gold Medal and about £30 in Money, will be awarded in the Session 1939–1940 for the "best communication on a scientific subject, communicated,* in the first instance, to the Royal Society of Edinburgh during the Sessions 1937–1938 and 1938–1939." Preference will be given to a Paper containing a discovery. (See also Council's resolutions at the end of these regulations.)

II. MAKDOUGALL-BRISBANE PRIZE.

(*Amended June* 7, 1926.)

This Prize is to be awarded biennially by the Council of the Royal Society of Edinburgh to such person, for such purposes, for such objects, and in such manner as shall appear to them the most conducive to the promotion of the interests of science; with the *proviso* that the Council shall not be compelled to award the Prize unless there shall be some individual engaged in scientific pursuit, or some Paper written on a scientific subject, or some discovery in science made during the biennial period, of sufficient merit or importance in the opinion of the Council to be entitled to the Prize.

1. The Prize, consisting of a Gold Medal and a sum of Money, will be awarded before the close of the Session 1940–1941, for an Essay, Paper, or other work having reference to any branch of scientific inquiry, either material or mental.
2. It is open to all men of science.
3. The specific subjects taken into consideration in the current award are governed by the resolutions of the Council as stated at the end of these regulations.
4. For the current period the Committee is representative of Group *A*.
5. The Committee will consider Papers presented to the Society within the Sessions 1938–1939 and 1939–1940, and will make a recommendation.

It is empowered to recommend either:—

(*a*) An award to the Author of an Essay or Paper considered as above, or
(*b*) That no award be made on the ground that, within its group, no Paper of sufficient merit has been presented, or

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* For the purposes of this award the word "communicated" shall be understood to mean the date on which the manuscript of a Paper is received in its final form for printing, as recorded by the General Secretary or other responsible official.

(*c*) That the Prize be awarded to some distinguished man of learning, who may not have presented a Paper to the Society within the period considered, but who is willing to deliver an address.

III. NEILL PRIZE.

The Council of the Royal Society of Edinburgh having received the bequest of the late Dr PATRICK NEILL of the sum of £500, for the purpose of "the interest thereof being applied in furnishing a Medal or other reward every second or third year to any distinguished Scottish Naturalist, according as such Medal or reward shall be voted by the Council of the said Society," hereby intimate:—

1. The NEILL PRIZE, consisting of a Gold Medal, will be awarded during the Session 1939–1940.

2. The Prize will be given for a Paper of distinguished merit, on a subject of Natural History, by a Scottish Naturalist, which shall have been presented * to the Society during the two years preceding the fourth Monday in October 1939,—or failing presentation of a Paper sufficiently meritorious, it will be awarded for a work or publication by some distinguished Scottish Naturalist, on some branch of Natural History, bearing date within five years of the time of award. (See also resolutions of Council at the end of these regulations.)

IV. GUNNING VICTORIA JUBILEE PRIZE.

This Prize, founded in the year 1887 by Dr R. H. GUNNING, is to be awarded quadrennially by the Council of the Royal Society of Edinburgh, in recognition of original work in Physics, Chemistry, or Pure or Applied Mathematics.

Evidence of such work may be afforded either by a Paper presented * to the Society, or by a Paper on one of the above subjects, or some discovery in them elsewhere communicated or made, which the Council may consider to be deserving of the Prize.

The Prize consists of a sum of money, and is open to men of science resident in or connected with Scotland. The first award was made in the year 1887. The next award will be made in Session 1940–1941.

In accordance with the wish of the Donor, the Council of the Society may on fit occasions award the Prize for work of a definite kind to be undertaken during the three succeeding years by a scientific man of recognised ability.

V. JAMES SCOTT PRIZE.

This Prize, founded in the year 1918 by the Trustees of the JAMES SCOTT Bequest, is to be awarded triennially, or at such intervals as the Council of the Royal Society of Edinburgh may decide, "for a lecture or essay on the fundamental concepts of Natural Philosophy."

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* For the purposes of this award the word "presented" shall be understood to mean the date on which the manuscript of a Paper is received in its final form for printing, as recorded by the General Secretary or other responsible official.

VI. BRUCE PRIZE.

The Society is trustee of a fund, instituted in 1923, to commemorate the work of Dr W. S. BRUCE as an explorer and scientific investigator in polar regions.

The Committee of Award is appointed jointly by the Royal Society of Edinburgh, the Royal Physical Society, and the Royal Scottish Geographical Society.

The Prize consists of a Bronze Medal and sum of Money. It is open to workers of all nationalities, with a preference, *ceteris paribus*, for those of Scottish birth or origin, and is to be awarded biennially for some notable contribution to Natural Sciences, such as Zoology, Botany, Geology, Meteorology, Oceanography, and Geography; the contribution to be in the nature of new knowledge, the outcome of a personal visit to polar regions on the part of the recipient. The recipient shall preferably be at the outset of his career as an investigator.

The next award will be made in 1940. Papers for the consideration of the Committee should be in the hands of the General Secretary of the Royal Society, 22 George Street, Edinburgh 2, not later than March 31 of that year.

VII. BRUCE-PRELLER LECTURE FUND.

The Council of the Royal Society of Edinburgh having received in 1929 the bequest of the late Dr CHARLES DU RICHE PRELLER of the sum of £500, decided that the income thereof be applied by the Council biennially as an honorarium for a special BRUCE-PRELLER Lecture or Address by an outstanding man of science, its subject to be Geology or Electrical or Physical Science, or in the discretion of the Council some other branch of science. The next award will be made in Session 1940–1941.

VIII. DAVID ANDERSON-BERRY FUND.

The Council of the Royal Society of Edinburgh having received in the year 1930, free of duty, the capital sum of one thousand pounds (£1000), to be used in terms of the will of the late Dr DAVID ANDERSON-BERRY, dated 23rd April 1926, decided that the income thereof be applied triennially, "in the first place in the presentation of a gold medal, and in the second place in the payment of a sum of money to the winner for the year of such gold medal, the winner being the person who, in the opinion of the Society, shall be the producer for the year of the best essay on the nature of X-rays and their therapeutical effect on human diseases."

The third award will be made in July 1941.

RESOLUTIONS OF COUNCIL IN REGARD TO THE MODE OF AWARDING PRIZES.

(*See Minutes of Meeting of January* 18, 1915.)

I. With regard to the Keith and Makdougall-Brisbane Prizes, which are open to all Sciences, the mode of award will be as follows:—

1. Papers or essays to be considered shall be arranged in two groups, *A* and *B*—Group *A* to include Astronomy, Chemistry, Mathematics, Metallurgy, Meteorology, and Physics; Group *B* to include Anatomy, Anthropology, Botany, Geology, Pathology, Physiology, and Zoology.
2. These two prizes shall be awarded to each group in alternate biennial periods, provided Papers worthy of recommendation have been communicated to the Society.
3. Prior to the adjudication the Council shall appoint, in the first instance, a Committee composed of representatives of the group of Sciences which did not receive the award in the immediately preceding period. The Committee shall consider the Papers which come within their group of Sciences, and report in due course to the Council.
4. In the event of the aforesaid Committee reporting that within their group of subjects there is, in their opinion, no Paper worthy of being recommended for the award, the Council, on accepting this report, shall appoint a Committee representative of the alternate group to consider Papers coming within their group and to report accordingly.
5. Papers to be considered by the Committees shall fall within the period dating from the last award in Groups *A* and *B* respectively.

II. With regard to the Neill Prize, the term "Naturalist" shall be understood to include any student in the Sciences composing Group *B*, namely, Anatomy, Anthropology, Botany, Geology, Pathology, Physiology, Zoology.

AWARDS OF THE KEITH, MAKDOUGALL-BRISBANE, NEILL, GUNNING, JAMES SCOTT, BRUCE, AND DAVID ANDERSON-BERRY PRIZES, AND THE BRUCE-PRELLER LECTURE FUND.

I. KEITH PRIZE.

1st Biennial Period, 1827–29.—Dr Brewster, for his papers "on his Discovery of Two New Immiscible Fluids in the Cavities of certain Minerals," published in the Transactions of the Society.

2nd Biennial Period, 1829–31.—Dr Brewster, for his paper "on a New Analysis of Solar Light," published in the Transactions of the Society.

3rd Biennial Period, 1831–33.—Thomas Graham, Esq., for his paper "on the Law of the Diffusion of Gases," published in the Transactions of the Society.

4th Biennial Period, 1833–35.—Professor J. D. Forbes, for his paper "on the Refraction and Polarization of Heat," published in the Transactions of the Society.

5th Biennial Period, 1835–37.—John Scott Russell, Esq., for his researches "on Hydrodynamics," published in the Transactions of the Society.

6th Biennial Period, 1837–39.—Mr John Shaw, for his experiments "on the Development and Growth of the Salmon," published in the Transactions of the Society.

7th Biennial Period, 1839–41.—Not awarded.

8th Biennial Period, 1841–43.—Professor James David Forbes, for his papers "on Glaciers," published in the Proceedings of the Society.

9th Biennial Period, 1843–45.—Not awarded.

10th Biennial Period, 1845–47.—General Sir Thomas Brisbane, Bart., for the Makerstoun Observations on Magnetic Phenomena, made at his expense, and published in the Transactions of the Society.

11th Biennial Period, 1847–49.—Not awarded.

12th Biennial Period, 1849–51.—Professor Kelland, for his papers "on General Differentiation, including his more recent Communication on a process of the Differential Calculus, and its application to the solution of certain Differential Equations," published in the Transactions of the Society.

13th Biennial Period, 1851–53.—W. J. Macquorn Rankine, Esq., for his series of papers "on the Mechanical Action of Heat," published in the Transactions of the Society.

14th Biennial Period, 1853–55.—Dr Thomas Anderson, for his papers "on the Crystalline Constituents of Opium, and on the Products of the Destructive Distillation of Animal Substances," published in the Transactions of the Society.

15th Biennial Period, 1855–57.—Professor Boole, for his Memoir "on the Application of the Theory of Probabilities to Questions of the Combination of Testimonies and Judgments," published in the Transactions of the Society.

16th Biennial Period, 1857–59.—Not awarded.

17th Biennial Period, 1859–61.—John Allan Broun, Esq., F.R.S., Director of the Trevandrum Observatory, for his papers "on the Horizontal Force of the Earth's Magnetism, on the Correction of the Bifilar Magnetometer, and on Terrestrial Magnetism generally," published in the Transactions of the Society.

18th Biennial Period, 1861–63.—Professor William Thomson, of the University of Glasgow, for his Communication "on some Kinematical and Dynamical Theorems."

19th Biennial Period, 1863–65.—Principal Forbes, St Andrews, for his "Experimental Inquiry into the Laws of Conduction of Heat in Iron Bars," published in the Transactions of the Society.

20th Biennial Period, 1865–67.—Professor C. Piazzi Smyth, for his paper "on Recent Measures at the Great Pyramid," published in the Transactions of the Society.

21ST BIENNIAL PERIOD, 1867–69.—Professor P. G. TAIT, for his paper "on the Rotation of a Rigid Body about a Fixed Point," published in the Transactions of the Society.

22ND BIENNIAL PERIOD, 1869–71.—Professor CLERK MAXWELL, for his paper "on Figures, Frames, and Diagrams of Forces," published in the Transactions of the Society.

23RD BIENNIAL PERIOD, 1871–73.—Professor P. G. TAIT, for his paper entitled "First Approximation to a Thermo-electric Diagram," published in the Transactions of the Society.

24TH BIENNIAL PERIOD, 1873–75.—Professor CRUM BROWN, for his Researches "on the Sense of Rotation, and on the Anatomical Relations of the Semicircular Canals of the Internal Ear."

25TH BIENNIAL PERIOD, 1875–77.—Professor M. FORSTER HEDDLE, for his papers "on the Rhombohedral Carbonates," and "on the Felspars of Scotland," published in the Transactions of the Society.

26TH BIENNIAL PERIOD, 1877–79.—Professor H. C. FLEEMING JENKIN, for his paper "on the Application of Graphic Methods to the Determination of the Efficiency of Machinery," published in the Transactions of the Society; Part II having appeared in the volume for 1877–78.

27TH BIENNIAL PERIOD, 1879–81.—Professor GEORGE CHRYSTAL, for his paper "on the Differential Telephone," published in the Transactions of the Society.

28TH BIENNIAL PERIOD, 1881–83.—THOMAS MUIR, Esq., LL.D., for his "Researches into the Theory of Determinants and Continued Fractions," published in the Proceedings of the Society.

29TH BIENNIAL PERIOD, 1883–85.—JOHN AITKEN, Esq., for his paper "on the Formation of Small Clear Spaces in Dusty Air," and for previous papers on Atmospheric Phenomena, published in the Transactions of the Society.

30TH BIENNIAL PERIOD, 1885–87.—JOHN YOUNG BUCHANAN, Esq., for a series of communications, extending over several years, on subjects connected with Ocean Circulation, Compressibility of Glass, etc.; two of which, viz., "On Ice and Brines," and "On the Distribution of Temperature in the Antarctic Ocean," have been published in the Proceedings of the Society.

31ST BIENNIAL PERIOD, 1887–89.—Professor E. A. LETTS, for his papers on the Organic Compounds of Phosphorus, published in the Transactions of the Society.

32ND BIENNIAL PERIOD, 1889–91.—R. T. OMOND, Esq., for his contributions to Meteorological Science, many of which are contained in vol. xxxiv of the Society's Transactions.

33RD BIENNIAL PERIOD, 1891–93.—Professor THOMAS R. FRASER, F.R.S., for his papers on *Strophanthus hispidus*, Strophanthin, and Strophanthidin, read to the Society in February and June 1889 and in December 1891, and printed in vols. xxxv, xxxvi, and xxxvii of the Society's Transactions.

34TH BIENNIAL PERIOD, 1893–95.—Dr CARGILL G. KNOTT, for his papers on the Strains produced by Magnetism in Iron and in Nickel, which have appeared in the Transactions and Proceedings of the Society.

35TH BIENNIAL PERIOD, 1895–97.—Dr THOMAS MUIR, for his continued communications on Determinants and Allied Questions.

36TH BIENNIAL PERIOD, 1897–99.—Dr JAMES BURGESS, for his paper "on the Definite Integral $\frac{2}{\sqrt{\pi}}\int_0^t \epsilon^{-t^2}dt$, with extended Tables of Values," printed in vol. xxxix of the Transactions of the Society.

37TH BIENNIAL PERIOD, 1899–1901.—Dr HUGH MARSHALL, for his discovery of the Persulphates, and for his Communications on the Properties and Reactions of these Salts, published in the Proceedings of the Society.

38TH BIENNIAL PERIOD, 1901–03.—Sir WILLIAM TURNER, K.C.B., LL.D., F.R.S., etc., for his memoirs entitled "A Contribution to the Craniology of the People of Scotland," published in the Transactions of the Society, and for his "Contributions to the Craniology of the People of the Empire of India," Parts I, II, likewise published in the Transactions of the Society.

39TH BIENNIAL PERIOD, 1903–05.—THOMAS H. BRYCE, M.A., M.D., for his two papers on "The Histology of the Blood of the Larva of *Lepidosiren paradoxa*," published in the Transactions of the Society within the period.

40TH BIENNIAL PERIOD, 1905–07.—ALEXANDER BRUCE, M.A., M.D., F.R.C.P.E., for his paper entitled "Distribution of the Cells in the Intermedio-Lateral Tract of the Spinal Cord," published in the Transactions of the Society within the period.

41ST BIENNIAL PERIOD, 1907–09.—WHEELTON HIND, M.D., B.S., F.R.C.S., F.G.S., for a paper published in the Transactions of the Society, "On the Lamellibranch and Gasteropod Fauna found in the Millstone Grit of Scotland."

42ND BIENNIAL PERIOD, 1909–11.—Professor ALEXANDER SMITH, B.Sc., Ph.D., of New York, for his researches upon "Sulphur" and upon "Vapour Pressure," appearing in the Proceedings of the Society.

43RD BIENNIAL PERIOD, 1911–13.—JAMES RUSSELL, Esq., for his series of investigations relating to magnetic phenomena in metals and the molecular theory of magnetism, the results of which have been published in the Proceedings and Transactions of the Society, the last paper having been issued within the period.

44TH BIENNIAL PERIOD, 1913–15.—JAMES HARTLEY ASHWORTH, D.Sc., for his papers on "Larvæ of Lingula and Pelagodiscus," and on "Sclerocheilus," published in the Transactions of the Society, and for other papers on the Morphology and Histology of Polychæta.

45TH BIENNIAL PERIOD, 1915–17.—ROBERT C. MOSSMAN, Esq., for his work on the Meteorology of the Antarctic Regions, which originated with the important series of observations made by him during the voyage of the "Scotia" (1902–1904), and includes his paper "On a Sea-Saw of Barometric Pressure, Temperature, and Wind Velocity between the Weddell Sea and the Ross Sea," published in the Proceedings of the Society.

46TH BIENNIAL PERIOD, 1917–19.—JOHN STEPHENSON, Lt.-Col., I.M.S., for his series of papers on the Oligochæta and other Annelida, several of which have been published in the Transactions of the Society.

47TH BIENNIAL PERIOD, 1919–21.—RALPH ALLEN SAMPSON, F.R.S., for his Astronomical Researches, including the papers "Studies in Clocks and Time-keeping: No. 1, Theory of the Maintenance of Motion; No. 2, Tables of the Circular Equation," published in the Proceedings of the Society within the period of the award.

48TH BIENNIAL PERIOD, 1921–23.—JOHN WALTER GREGORY, F.R.S., for his papers published in the Transactions of the Society, and in recognition of his numerous contributions to Geology, extending over a period of thirty-six years.

49TH BIENNIAL PERIOD, 1923–25.—HERBERT WESTREN TURNBULL, M.A., for the papers on "Hyper-Algebra," "Invariant Theory," and "Algebraic Geometry," three of which have been published in the Proceedings within the period of award.

50TH BIENNIAL PERIOD, 1925–27.—THOMAS JOHN JEHU, M.A., M.D., F.G.S., and ROBERT MELDRUM CRAIG, M.A., B.Sc., F.G.S., for the joint series of papers which have recently appeared in the Transactions of the Society on the "Geology of the Outer Hebrides."

51ST BIENNIAL PERIOD, 1927–29.—CHRISTINA C. MILLER, B.Sc., Ph.D., for her papers on the "Slow Oxidation of Phosphorus Trioxide," published in the Proceedings within the period of the award, and in consideration of subsequent developments on "Slow Oxidation of Phosphorus," published elsewhere.

52ND BIENNIAL PERIOD, 1929–31.—ALAN WILLIAM GREENWOOD, M.Sc., Ph.D., for his papers on the "Biology of the Fowl," several of which have appeared in the Proceedings within the period of award.

53RD BIENNIAL PERIOD, 1931–33.—A. CRICHTON MITCHELL, D.Sc., for his paper "On the Diurnal Incidence of Disturbance in the Terrestrial Magnetic Field," published in the Transactions within the period of award.

54TH BIENNIAL PERIOD, 1933–35.—LANCELOT T. HOGBEN, D.Sc., F.R.S., for his papers on genetical subjects, published alone and in collaboration, which have appeared in the Proceedings within the period of award.

55TH BIENNIAL PERIOD, 1935–37.—HAROLD STANLEY RUSE, M.A., for his paper "On the Geometry of Dirac's Equations and their Expression in Tensor Forms," published in the Proceedings within the period, and for his other papers in the Proceedings.

II. MAKDOUGALL-BRISBANE PRIZE.

1ST BIENNIAL PERIOD, 1859.—Sir RODERICK IMPEY MURCHISON, on account of his Contributions to the Geology of Scotland.

2ND BIENNIAL PERIOD, 1860–62.—WILLIAM SELLER, M.D., F.R.C.P.E., for his "Memoir of the Life and Writings of Dr Robert Whytt," published in the Transactions of the Society.

3rd Biennial Period, 1862–64.—John Denis Macdonald, Esq., R.N., F.R.S., Surgeon of H.M.S. "Icarus," for his paper "on the Representative Relationships of the Fixed and Free Tunicata, regarded as Two Sub-classes of equivalent value; with some General Remarks on their Morphology," published in the Transactions of the Society.

4th Biennial Period, 1864–66.—Not awarded.

5th Biennial Period, 1866–68.—Dr Alexander Crum Brown and Dr Thomas Richard Fraser, for their conjoint paper "on the Connection between Chemical Constitution and Physiological Action," published in the Transactions of the Society.

6th Biennial Period, 1868–70.—Not awarded.

7th Biennial Period, 1870–72.—George James Allman, M.D., F.R.S., Emeritus Professor of Natural History, for his paper "on the Homological Relations of the Cœlenterata," published in the Transactions, which forms a leading chapter of his Monograph of Gymnoblastic or Tubularian Hydroids—since published.

8th Biennial Period, 1872–74.—Professor Lister, for his paper "on the Germ Theory of Putrefaction and the Fermentive Changes," communicated to the Society, 7th April 1873.

9th Biennial Period, 1874–76.—Alexander Buchan, A.M., for his paper "on the Diurnal Oscillation of the Barometer," published in the Transactions of the Society.

10th Biennial Period, 1876–78.—Professor Archibald Geikie, for his paper "on the Old Red Sandstone of Western Europe," published in the Transactions of the Society.

11th Biennial Period, 1878–80.—Professor Piazzi Smyth, Astronomer-Royal for Scotland, for his paper "on the Solar Spectrum in 1877–78, with some Practical Idea of its probable Temperature of Origination," published in the Transactions of the Society.

12th Biennial Period, 1880–82.—Professor James Geikie, for his "Contributions to the Geology of the North-West of Europe," including his paper "on the Geology of the Faroes," published in the Transactions of the Society.

13th Biennial Period, 1882–84.—Edward Sang, Esq., LL.D., for his paper "on the Need of Decimal Subdivisions in Astronomy and Navigation, and on Tables requisite therefor," and generally for his Recalculations of Logarithms both of Numbers and Trigonometrical Ratios—the former communication being published in the Proceedings of the Society.

14th Biennial Period, 1884–86.—John Murray, Esq., LL.D., for his papers "On the Drainage Areas of Continents and Ocean Deposits," "The Rainfall of the Globe, and Discharge of Rivers," "The Height of the Land and Depth of the Ocean," and "The Distribution of Temperature in the Scottish Lochs as affected by the Wind."

15th Biennial Period, 1886–88.—Archibald Geikie, Esq., LL.D., for numerous Communications, especially that entitled "History of Volcanic Action during the Tertiary Period in the British Isles," published in the Transactions of the Society.

16th Biennial Period, 1888–90.—Dr Ludwig Becker, for his paper on "The Solar Spectrum at Medium and Low Altitudes," printed in vol. xxxvi, Part I, of the Society's Transactions.

17th Biennial Period, 1890–92.—Hugh Robert Mill, Esq., D.Sc., for his papers on "The Physical Conditions of the Clyde Sea Area," Part I being already published in vol. xxxvi of the Society's Transactions.

18th Biennial Period, 1892–94.—Professor James Walker, D.Sc., Ph.D., for his work on Physical Chemistry, part of which has been published in the Proceedings of the Society, vol. xx, pp. 255–263. In making this award, the Council took into consideration the work done by Professor Walker along with Professor Crum Brown on the Electrolytic Synthesis of Dibasic Acids, published in the Transactions of the Society.

19th Biennial Period, 1894–96.—Professor John G. M'Kendrick, for numerous Physiological papers, especially in connection with Sound, many of which have appeared in the Society's publications.

20th Biennial Period, 1896–98.—Dr William Peddie, for his papers on the Torsional Rigidity of Wires.

21st Biennial Period, 1898–1900.—Dr Ramsay H. Traquair, for his paper entitled "Report on Fossil Fishes collected by the Geological Survey in the Upper Silurian Rocks of Scotland," printed in vol. xxxix of the Transactions of the Society.

22nd Biennial Period, 1900–02.—Dr Arthur T. Masterman, for his paper entitled "The Early Development of *Cribrella oculata* (Forbes), with remarks on Echinoderm Development," printed in vol. xl of the Transactions of the Society.

23rd Biennial Period, 1902–04.—John Dougall, M.A., for his paper on "An Analytical Theory of the Equilibrium of an Isotropic Elastic Plate," published in vol. xli of the Transactions of the Society.

24TH BIENNIAL PERIOD, 1904–06.—JACOB E. HALM, Ph.D., for his two papers entitled "Spectroscopic Observations of the Rotation of the Sun," and "Some Further Results obtained with the Spectroheliometer," and for other astronomical and mathematical papers published in the Transactions and Proceedings of the Society within the period.

25TH BIENNIAL PERIOD, 1906–08.—D. T. GWYNNE-VAUGHAN, M.A., F.L.S., for his papers, 1st, "On the Fossil Osmundaceæ," and 2nd, "On the Origin of the Adaxially-curved Leaf-trace in the Filicales," communicated by him conjointly with Dr R. Kidston.

26TH BIENNIAL PERIOD, 1908–10.—ERNEST MACLAGAN WEDDERBURN, M.A., LL.B., for his series of papers bearing upon "The Temperature Distribution in Fresh-water Lochs," and especially upon "The Temperature Seiche."

27TH BIENNIAL PERIOD, 1910–12.—JOHN BROWNLEE, M.A., M.D., D.Sc., for his contributions to the Theory of Mendelian Distributions and cognate subjects, published in the Proceedings of the Society within and prior to the prescribed period.

28TH BIENNIAL PERIOD, 1912–14.—Professor C. R. MARSHALL, M.A., M.D., for his studies "On the Pharmacological Action of Tetra-alkyl-ammonium Compounds."

29TH BIENNIAL PERIOD, 1914–16.—ROBERT ALEXANDER HOUSTOUN, Ph.D., D.Sc., for his series of papers on "The Absorption of Light by Inorganic Salts," published in the Proceedings of the Society.

30TH BIENNIAL PERIOD, 1916–18.—Professor A. ANSTRUTHER LAWSON, for his Memoirs on "The Prothalli of *Tmesipteris Tannensis* and of *Psilotum*," published in the Transactions of the Society, together with previous papers on Cytology and on The Gametophytes of various Gymnosperms.

31ST BIENNIAL PERIOD, 1918–20.—Professor J. H. MACLAGAN WEDDERBURN of Princeton University, for his Memoirs in Universal Algebra, etc., published in the Transactions and Proceedings of the Society, and elsewhere.

32ND BIENNIAL PERIOD, 1920–22.—Professor W. T. GORDON, M.A., D.Sc., for his paper on "Cambrian Organic Remains from a Dredging in the Weddell Sea," published in the Transactions of the Society within the period, and for his investigations on the Fossil Flora of the Pettycur Limestone, previously published in the Transactions.

33RD BIENNIAL PERIOD, 1922–24.—Professor H. STANLEY ALLEN, D.Sc., for his papers on the "Quantum and Atomic Theory," published in the Society's Proceedings within the period.

34TH BIENNIAL PERIOD, 1924–26.—CHARLES MORLEY WENYON, C.M.G., C.B.E., F.R.S., for his distinguished work in Protozoology extending over a period of twenty-one years.

35TH BIENNIAL PERIOD, 1926–28.—W. O. KERMACK, M.A., D.Sc., for his contributions to Chemistry, published in the Society's Proceedings and elsewhere.

36TH BIENNIAL PERIOD, 1928–30.—NELLIE B. EALES, D.Sc., for her papers in the Society's Transactions on "The Anatomy of a Fœtal African Elephant."

37TH BIENNIAL PERIOD, 1930–32.—A. C. AITKEN, M.A., D.Sc., for various contributions to Mathematics, published in the Society's Proceedings and elsewhere.

38TH BIENNIAL PERIOD, 1932–34.—A. E. CAMERON, M.A., D.Sc., for his publications in Entomology, including his paper in the Transactions, "The Life-History and Structure of *Hæmatopota pluvialis* Linné (Tabanidæ)."

39TH BIENNIAL PERIOD, 1934–36.—E. M. ANDERSON, M.A., D.Sc., for his paper "The Dynamics of the Formation of Cone-sheets, Ring-dykes, and Caldron-subsidences," published in the Society's Proceedings within the period.

III. THE NEILL PRIZE.

1ST TRIENNIAL PERIOD, 1856–59.—Dr W. LAUDER LINDSAY, for his paper "on the Spermogones and Pycnides of Filamentous, Fruticulose, and Foliaceous Lichens," published in the Transactions of the Society.

2ND TRIENNIAL PERIOD, 1859–62.—ROBERT KAYE GREVILLE, LL.D., for his contributions to Scottish Natural History, more especially in the department of Cryptogamic Botany, including his recent papers on Diatomaceæ.

3RD TRIENNIAL PERIOD, 1862–65.—ANDREW CROMBIE RAMSAY, F.R.S., Professor of Geology in the Government School of Mines, and Local Director of the Geological Survey of Great Britain, for his various works and memoirs published during the last five years, in which he has applied the large experience acquired by him in the Direction of the arduous work of the Geological Survey of Great Britain to the elucidation of important questions bearing on Geological Science.

4TH Triennial Period, 1865–68.—Dr William Carmichael M'Intosh, for his paper "on the Structure of the British Nemerteans, and on some New British Annelids," published in the Transactions of the Society.

5TH Triennial Period, 1868–71.—Professor William Turner, for his papers "on the Great Finner Whale; and on the Gravid Uterus, and the Arrangement of the Fœtal Membranes in the Cetacea," published in the Transactions of the Society.

6TH Triennial Period, 1871–74.—Charles William Peach, Esq., for his Contributions to Scottish Zoology and Geology, and for his recent contributions to Fossil Botany.

7TH Triennial Period, 1874–77.—Dr Ramsay H. Traquair, for his paper "on the Structure and Affinities of *Tristichopterus alatus* (Egerton)," published in the Transactions of the Society, and also for his contributions to the Knowledge of the Structure of Recent and Fossil Fishes.

8TH Triennial Period, 1877–80.—John Murray, Esq., for his paper "on the Structure and Origin of Coral Reefs and Islands," published (in abstract) in the Proceedings of the Society.

9TH Triennial Period, 1880–83.—Professor W. A. Herdman, for his papers "on the Tunicata," published in the Proceedings and Transactions of the Society.

10TH Triennial Period, 1883–86.—B. N. Peach, Esq., for his Contributions to the Geology and Palæontology of Scotland, published in the Transactions of the Society.

11TH Triennial Period, 1886–89.—Robert Kidston, Esq., for his Researches in Fossil Botany, published in the Transactions of the Society.

12TH Triennial Period, 1889–92.—John Horne, Esq., F.G.S., for his Investigations into the Geological Structure and Petrology of the North-West Highlands.

13TH Triennial Period, 1892–95.—Robert Irvine, Esq., for his papers on the Action of Organisms in the Secretion of Carbonate of Lime and Silica, and on the solution of these substances in Organic Juices. These are printed in the Society's Transactions and Proceedings.

14TH Triennial Period, 1895–98.—Professor J. Cossar Ewart, for his recent Investigations connected with Telegony.

15TH Triennial Period, 1898–1901.—Dr John S. Flett, for his papers entitled "The Old Red Sandstone of the Orkneys" and "The Trap Dykes of the Orkneys," printed in vol. xxxix of the Transactions of the Society.

16TH Triennial Period, 1901–04.—Professor J. Graham Kerr, M.A., for his Researches on *Lepidosiren paradoxa*, published in the Philosophical Transactions of the Royal Society, London.

17TH Triennial Period, 1904–07.—Frank J. Cole, B.Sc., for his paper entitled "A Monograph on the General Morphology of the Myxinoid Fishes, based on a Study of Myxine," published in the Transactions of the Society, regard being also paid to Mr Cole's other valuable contributions to the Anatomy and Morphology of Fishes.

1ST Biennial Period, 1907–09.—Francis J. Lewis, M.Sc., F.L.S., for his papers in the Society's Transactions "On the Plant Remains of the Scottish Peat Mosses."

2ND Biennial Period, 1909–11.—James Murray, Esq., for his paper on "Scottish Rotifers collected by the Lake Survey (Supplement)," and other papers on the "Rotifera" and "Tardigrada," which appeared in the Transactions of the Society—(this Prize was awarded after consideration of the papers received within the five years prior to the time of award: see Neill Prize Regulations).

3RD Biennial Period, 1911–13.—W. S. Bruce, LL.D., in recognition of the scientific results of his Arctic and Antarctic explorations.

4TH Biennial Period, 1913–15.—Robert Campbell, D.Sc., for his paper on "The Upper Cambrian Rocks at Craigeven Bay, Stonehaven," and "Downtonian and Old Red Sandstone Rocks of Kincardineshire," published in the Transactions of the Society.

5TH Biennial Period, 1915–17.—W. H. Lang, F.R.S., M.B., D.Sc., for his paper in conjunction with Dr R. Kidston, F.R.S., on *Rhynia Gwynne-Vaughani*, Kidston and Lang, published in the Transactions of the Society, and for his previous investigations on Pteridophytes and Cycads.

6TH Biennial Period, 1917–19.—John Tait, D.Sc., M.D., for his work on Crustacea, published in the Proceedings of the Society, and for his papers on the blood of Crustacea.

7TH Biennial Period, 1919–21.—Sir Edward A. Sharpey-Schafer, F.R.S., for his recent contributions to our knowledge of Physiology, and in recognition of his published work extending over a period of fifty years.

8th Biennial Period, 1921–23.—John M'Lean Thompson, M.A., D.Sc., University of Liverpool, for his series of Memoirs on Staminal Zygomorphy, and on the Anatomy of the Filicales.

9th Biennial Period, 1923–25.—Frederick Orpen Bower, F.R.S., for his recent contributions to Botanical knowledge and in recognition of his published work extending over a period of forty-five years.

10th Biennial Period, 1925–27.—Arthur Robinson, M.D., M.R.C.S., for his contributions to Comparative Anatomy and Embryology.

11th Biennial Period, 1927–29.—Edward Battersby Bailey, M.C., F.R.S., in recognition of his valuable contributions to the Geology of Scotland, two of which have recently appeared in the Transactions of the Society.

12th Biennial Period, 1929–31.—Charles Henry O'Donoghue, D.Sc., for his papers on the "Blood Vascular System," and for his earlier work on the "Morphology of the *corpus luteum*."

13th Biennial Period. 1931–33.—George Walter Tyrrell, A.R.C.S., D.Sc., for his contributions to the Geology and Petrology of Sub-Arctic and Sub-Antarctic Lands.

14th Biennial Period, 1933–35.—Samuel Williams, Ph.D., for his contributions to the Anatomy and Experimental Morphology of the Pteridophyta.

15th Biennial Period, 1935–37.—William J. Hamilton, M.D., D.Sc., for his contributions to the Embryology of the Ferret and other work published in the Transactions.

IV. GUNNING VICTORIA JUBILEE PRIZE.

1st Triennial Period, 1884–87.—Sir William Thomson, Pres. R.S.E., F.R.S., for a remarkable series of papers "on Hydrokinetics," especially on Waves and Vortices which have been communicated to the Society.

2nd Triennial Period, 1887–90.—Professor P. G. Tait, Sec. R.S.E., for his work in connection with the "Challenger" Expedition, and his other Researches in Physical Science.

3rd Triennial Period, 1890–93.—Alexander Buchan, Esq., LL.D., for his varied, extensive, and extremely important Contributions to Meteorology, many of which have appeared in the Society's publications.

4th Triennial Period, 1893–96.—John Aitken, Esq., for his brilliant Investigations in Physics, especially in connection with the Formation and Condensation of Aqueous Vapour.

1st Quadrennial Period, 1896–1900.—Dr T. D. Anderson, for his discoveries of New and Variable Stars.

2nd Quadrennial Period, 1900–04.—Sir James Dewar, LL.D., D.C.L., F.R.S., etc., for his researches on the Liquefaction of Gases, extending over the last quarter of a century, and on the Chemical and Physical Properties of Substances at Low Temperatures: his earliest papers being published in the Transactions and Proceedings of the Society.

3rd Quadrennial Period, 1904–08.—Professor George Chrystal, M.A., LL.D., for a series of papers on "Seiches," including "The Hydrodynamical Theory and Experimental Investigations of the Seiche Phenomena of Certain Scottish Lakes."

4th Quadrennial Period, 1908–12.—Professor J. Norman Collie, Ph.D., F.R.S., for his distinguished contributions to Chemistry, Organic and Inorganic, during twenty-seven years, including his work upon Neon and other rare gases. Professor Collie's early papers were contributed to the Transactions of the Society.

5th Quadrennial Period, 1912–16.—Sir Thomas Muir, C.M.G., LL.D., F.R.S., for his series of Memoirs upon "The Theory and History of Determinants and Allied Forms," published in the Transactions and Proceedings of the Society between the years 1872 and 1915.

6th Quadrennial Period, 1916–20.—C. T. R. Wilson, Esq., F.R.S., in recognition of his important discoveries in relation to Condensation Nuclei, Ionisation of Gases and Atmospheric Electricity.

7th Quadrennial Period, 1920–24.—Sir J. J. Thomson, O.M., F.R.S., in recognition of his great discoveries in Physical Science.

8th Quadrennial Period, 1924–28.—Professor E. T. Whittaker, F.R.S., in recognition of his distinguished contributions to Mathematical Science, and of his promotion of Mathematical Research in Scotland.

9TH QUADRENNIAL PERIOD, 1928–32.—Emeritus Professor Sir J. WALKER, F.R.S., for numerous contributions to Physical and General Chemistry.

10TH QUADRENNIAL PERIOD, 1932–36.—Professor C. G. DARWIN, F.R.S., for his distinguished contributions in Mathematical Physics.

V. JAMES SCOTT PRIZE.

1ST AWARD, 1918–22.—Professor A. N. WHITEHEAD, F.R.S., for his lecture delivered on June 5, 1922, on "The Relatedness of Nature."

2ND AWARD, 1922–27.—Sir JOSEPH LARMOR, M.A., D.Sc., LL.D., F.R.S., for his lecture delivered on July 4, 1927, on "The Grasp of Mind on Nature."

3RD AWARD, 1927–30.—Professor NIELS BOHR, for his lecture delivered on May 26, 1930, on "Philosophical Aspects of Atomic Theory."

4TH AWARD, 1930–33.—Professor Dr ARNOLD SOMMERFELD, for his lecture delivered on May 1, 1933, on "Ways to the Knowledge of Nature."

5TH AWARD, 1933–38.—Professor P. A. M. DIRAC, F.R.S., for his lecture delivered on February 6, 1939, on "The Relation between Mathematics and Physics."

VI. BRUCE PRIZE.

1ST AWARD, 1926.—JAMES MANN WORDIE, M.A., for his Oceanographical and Geological work in both Polar Regions.

2ND AWARD, 1928.—H. U. SVERDRUP, for his contributions to the knowledge of the Meteorology, Magnetism, and Tides of the Arctic, as an outcome of his travels with the Norwegian Expedition in the "Maud" from 1918 to 1925.

3RD AWARD, 1930.—N. A. MACKINTOSH, M.Sc., A.R.C.S., for his researches into the Biology of Whales in the Waters of the Falkland Islands Dependencies.

4TH AWARD, 1932.—HENRY GINO WATKINS, for important contributions to the topography of Spitsbergen, Labrador, and East Greenland, and investigation of the Ice Cap of Greenland.

5TH AWARD, 1936.—JAMES WILLIAM SLESSER MARR, M.A., B.Sc., for his work in the Southern Ocean and more particularly for his monograph on the South Orkney Islands.

6TH AWARD, 1938.—ALEXANDER R. GLEN, for his work in Spitsbergen, including Survey in New Friesland and the completion of the map of North East Land.

VII. BRUCE-PRELLER LECTURE FUND.

1ST AWARD, 1931.—Professor E. T. WHITTAKER, F.R.S., for his lecture, "James Clerk Maxwell and Mechanical Descriptions of the Universe."

2ND AWARD, 1933.—Professor C. H. LANDER, C.B.E., for his lecture on October 23, 1933, on "The Liquefaction of Coal."

3RD AWARD, 1935.—Professor W. L. BRAGG, O.B.E., F.R.S., for his lecture on February 4, 1935, on "The New Crystallography."

4TH AWARD, 1937.—Professor H. S. TAYLOR, F.R.S., for his lecture on June 7, 1937, on "Heavy Hydrogen in Scientific Research."

VIII. DAVID ANDERSON-BERRY FUND.

1ST AWARD, 1935.—CHARLES MELVILLE SCOTT, M.A., M.B., D.Sc., for his essay "On the Action of X- and Gamma-Rays on Living Cells."

2ND AWARD, 1938.—MARY A. C. COWELL, M.B., Holt Radium Institute, Manchester, for her essay "An Investigation into some of the Factors affecting the Response of Human Skin and Human Skin Tumours to Radiation."

ABSTRACT

OF

THE ACCOUNTS

OF

THE ROYAL SOCIETY OF EDINBURGH,

SESSION—1ST OCTOBER 1937 TO 30TH SEPTEMBER 1938.

E. MACLAGAN WEDDERBURN, O.B.E.,
D.K.S., LL.D.
Treasurer.

I. GENERAL FUND

1. *Funds as at 30th September* 1937, per last Account			£13,130 14 1
Deduct—Contributions in advance for 1937–38			9 9 0
			£13,121 5 1
2. *Commutation Fee Fund*—			
1 Fellow elected Session 1930–31			45 3 0
			£13,166 8 1
Add Income—			
1. *Contributions for current Session*—			
481 Fellows at £3, 3s. each	£1515 3 0		
Fees of Admission of forty New Fellows	126 0 0		
First Annual Contribution of forty-one New Fellows	129 3 0		
		£1770 6 0	
2. *Extra Contributions for* 1937–38 under Amended Law VI.—			
Voluntary Contributions	£41 19 0		
Commutation	10 10 0		
		52 9 0	
3. *Interest Received, Untaxed*—			
General Fund—			
On £2100 2½% Consolidated Stock	£52 10 0		
On £9742, 12s. 5d. 2¾% Guaranteed Stock	267 18 4		
On Deposit Receipts	7 0 4		
	£327 8 8		
Special Subscription Fund—			
On £936, 0s. 11d. 2¾% Guaranteed Stock (1933)	25 14 8		
R. M. Smith Legacy—			
On £554, 13s. 7d. 2¾% Guaranteed Stock (1933)	15 5 0		
Publication Fund—			
On £2568, 5s. 1d. 2¾% Guaranteed Stock (1933)	70 12 4		
Commutation Fee Fund—			
On £198, 8s. 11d. 2¾% Guaranteed Stock (1933)	5 9 0		
		444 9 8	
Forward		£2267 4 8	£13,166 8 1

Forward		£2267 4 8	£13,166 8 1
4. *Transactions and Proceedings sold*		136 17 10	
5. *Grants*—			
Annual Grant from Government	£600 0 0		
Grant from Royal Society from Government Publication Grant	300 0 0		
Grants from Trustees of the Carnegie Trust for the Universities of Scotland	203 19 3		
Other Sources	30 0 0		
		1133 19 3	
6. *Publication Fund*—Sale of Volumes		1 6 2	
			3,539 7 11
			£16,705 16 0
Deduct **Expenditure—**			
1. *Expenses of Transactions and Proceedings*—			
Transactions		£702 18 1	
Proceedings		584 11 9	
		£1287 9 10	
2. *Books, Periodicals, Newspapers, etc.*		243 7 1	
3. *Library Binding*		301 8 10	
4. *Reserve for Gregory Memorial Volume*		200 0 0	
5. *General Upkeep of Society's Rooms*—			
Insurance and Water Rates	£28 6 1		
Repairs and Furnishings	56 0 9		
Heating and Lighting	66 12 9		
Cleaning	17 13 0		
Caretaker's Salary and Uniform	164 3 10		
Charwoman's Wages	73 7 2		
		406 3 7	
6. *Management*—			
Honorarium to General Secretary	£100 0 0		
Salaries	545 0 0		
Fee to Treasurer's Clerk	35 0 0		
Society's Contribution to Staff Pension Fund under Universities Scheme	57 10 0		
State Insurance	4 2 4		
General Printing and Stationery	131 11 2		
Telephone	19 9 5		
Audit Fee	10 10 0		
Tea Expenses at Meetings	39 14 0		
Postages and Petty Outlays	59 15 6		
Miscellaneous	16 13 9		
		1019 6 2	
7. *Extraordinary Expenditure*—			
Staircase (West) Carpet, Final Payment	£37 18 6		
Installation and laying of Carpet	8 5 3		
Dinner to Professor Planck—Deficit	3 13 8		
Clerk Maxwell Inscription	12 0 0		
		61 17 5	
8. *Commutation Fee Fund*—			
Transferred to Special Fund (p. 316)	£45 3 0		
9. *Arrears of Contributions* written off as irrecoverable		37 16 0	
			3,557 8 11
Funds as at 30th September 1938			£13,148 7 1

Represented by—

£9742, 12s. 5d. 2½% Guaranteed Stock (1933) at cost		£8,298 1 9	
£2100 2½% Consolidated Stock at cost		1,113 0 0	
£554, 13s. 7d. 2½% Guaranteed Stock (1933) at cost—Robert Mackay Smith Legacy		472 8 9	
£2568, 5s. 1d. 2½% Guaranteed Stock (1933) at cost—Publication Fund (comprising Peter Guthrie Tait Memorial Fund and Dr John Aitken Fund)		2,187 9 1	
£936, 0s. 11d. 2½% Guaranteed Stock (1933) at cost—Special Subscription Fund		797 5 2	
£198, 8s. 11d. 2½% Guaranteed Stock (1933) at cost	£154 7 0		
Due by Union Bank of Scotland, Ltd., on Deposit Receipt	45 3 0		
Life Membership Commutation Fee Fund		199 10 0	
Arrears of Contribution at 30th September 1938—			
Present Session	£69 6 0		
Previous Session	25 4 0		
		94 10 0	
Due by Union Bank of Scotland, Ltd., on Current Account		180 11 4	
Cash—Imprest Amount		15 0 0	
		£13,357 16 1	
Less—Reserve for Gregory Memorial Volume	£200 0 0		
Contributions in Advance for 1938-39	9 9 0		
		209 9 0	
			£13,148 7 1

In addition the Society owns the Library, Museum, Pictures, etc., and Furniture in the Rooms 22 George Street, Edinburgh.

Note—

Income for current Session as per preceding Accounts		£3539 7 11
Add—Arrears of Contributions at 30th September 1937		116 11 0
		£3655 18 11
Deduct—*Expenditure* for current Session as per preceding Accounts	£3557 8 11	
Arrears of Contributions at 30th September 1938	94 10 0	
		3651 18 11
Surplus for year to 30th September 1938		£4 0 0

COMMUTATION FEE FUND.

Year to 30th September 1938.

Funds as at 30th September 1937, per last Account		£154 7 0
Fee received for Life Membership—		
1 Fellow elected 1930–31		45 3 0
Interest received on Investment		5 9 0
		£204 19 0
Deduct—		
Transferred to General Fund (Interest on Investment)		5 9 0
Total Funds (included in General Funds, above)		£199 10 0
Represented by—		
£198, 8s. 11d. 2½% Guaranteed Stock (1933) at cost	£154 7 0	
Due by Union Bank of Scotland, Ltd., on Deposit Receipt	45 3 0	
		199 10 0

PUBLICATION FUND.

(*Comprising Peter Guthrie Tait Memorial Fund and Dr John Aitken Fund.*)

Year to 30th September 1938.

Funds as at 30th September 1937, per last Account		£2187 9 1
Interest Received: Untaxed—		
Peter Guthrie Tait Memorial Fund—		
On £1929, 17s. 1d. 2½% Guaranteed Stock (1933)	£53 1 4	
Dr John Aitken Fund—		
On £638, 8s. 2½% Guaranteed Stock (1933)	17 11 0	
		70 12 4
Sale of Volumes, Dr John Aitken Fund		1 6 2
		£2259 7 7
Deduct—		
Transferred to General Fund to meet cost of Publication,		
Interest, p. 1	£70 12 4	
Sale of Volumes, p. 2	1 6 2	
		71 18 6
Total Funds (included in General Fund, p. 3)		£2187 9 1
Represented by—		
£2568, 5s. 1d. 2½% Guaranteed Stock (1933) at cost		£2187 9 1

II. PRIZE FUNDS

Year to 30th September 1938.

1. *Keith Fund*—			
Funds as at 30th September 1937, per last Account—			
£801, 13s. 4d. 2½% Guaranteed Stock (1933) at cost			£682 16 1
Balance due by Union Bank of Scotland, Ltd., on Deposit Receipt			65 10 4
			£748 6 5
Interest Received—On Investment		£22 0 10	
On Deposit Receipts		0 12 0	
			22 12 10
			£770 19 3
Deduct—Professor H. S. Ruse 1935-37 Award		£29 0 0	
Cost of Gold Medal		21 0 0	
			50 0 0
			£720 19 3
2. *Neill Fund*—			
Funds as at 30th September 1937, per last Account—			
£370 2½% Guaranteed Stock (1933) at cost		£315 2 9	
Balance due by Union Bank of Scotland, Ltd., on Deposit Receipt		28 14 2	
		£343 16 11	
Interest received—On Investment	£10 3 6		
On Deposit Receipts	0 4 8		
		10 8 2	
		£354 5 1	
Deduct—Cost of Gold Medal		21 0 0	
			333 5 1
3. *Makdougall-Brisbane Fund*—			
Funds as at 30th September 1937, per last Account—			
£493, 6s. 7d. 2½% Guaranteed Stock (1933) at cost		£420 3 8	
Balance due by Union Bank of Scotland, Ltd., on Deposit Receipt		38 12 7	
Forward		£458 16 3	£1054 4 4

Forward		£458 16 3	£1054 4 4
Interest received—On Investment	£13 11 2		
On Deposit Receipts	0 8 2		
		13 19 4	
			472 15 7
4. *Makerstoun Magnetic Meteorological Observation Fund*—			
Funds as at 30*th September* 1937, per last Account—			
£308, 6s. 9d. 2½% Guaranteed Stock (1933) at cost		£262 12 5	
Balance due by Union Bank of Scotland, Ltd., on Deposit Receipt		146 18 3	
		£409 10 8	
Interest received—On Investment	£8 9 6		
On Deposit Receipts	1 9 5		
		9 18 11	
			419 9 7
5. *Gunning Victoria Jubilee Prize Fund* (Instituted by Dr Gunning of Edinburgh and Rio de Janeiro)—			
Funds as at 30*th September* 1937, per last Account—			
£739, 12s. 5d. 2½% Guaranteed Stock (1933) at cost		£629 19 2	
Balance due by Union Bank of Scotland, Ltd., on Deposit Receipt		78 17 2	
		£708 16 4	
Interest received—On Investment	£20 6 8		
On Deposit Receipts	0 16 11		
		21 3 7	
			729 19 11
6. *James Scott Prize Fund*—			
Funds as at 30*th September* 1937, per last Account—			
£305, 5s. 2½% Guaranteed Stock (1933) at cost		£259 19 10	
Balance due by Union Bank of Scotland, Ltd., on Deposit Receipt		36 18 1	
		£296 17 11	
Interest received—On Investment	£8 7 10		
On Deposit Receipts	0 7 5		
		8 15 3	
			305 13 2
7. *Dr W. S. Bruce Memorial Fund*—			
Funds as at 30*th September* 1937, per last Account—			
£289, 1s. 5d. 2½% Guaranteed Stock (1933) at cost		£246 4 2	
Balance due by Union Bank of Scotland, Ltd., on Deposit Receipt		57 18 9	
		£304 2 11	
Interest received—On Investment	£7 18 10		
On Deposit Receipts	8 10		
		8 7 8	
		£312 10 7	
Deduct—J. W. S. Marr 1936 Award	£10 0 0		
Cost of Bronze Medal	0 15 0		
		10 15 0	
			301 15 7
8. *Bruce-Preller Lecture Fund*—			
Funds as at 30*th September* 1937, per last Account—			
£140, 9s. Royal Bank of Scotland Stock, taken over at 350%		£491 11 6	
Balance due by Union Bank of Scotland, Ltd., on Deposit Receipt		33 10 5	
Forward		£525 1 11	£3283 18 2

Forward		£525 1 11	£3283 18 2
Interest received—On Investment (less tax £6, 5s. 4d.)	£17 12 2		
On Deposit Receipts	0 8 0		
		18 0 2	
Repayment of Income Tax for year to December 1937		5 19 4	
			549 1 5
9. *Dr David Anderson-Berry Fund—*			
Funds as at 30th September 1937, per last Account—			
£1528, 0s. 4d. Local Loans 3% Stock at cost		£1000 0 0	
Balance due by Union Bank of Scotland, Ltd., on Deposit Receipt		81 11 7	
		£1081 11 7	
Interest received—On Investment	£45 16 8		
On Deposit Receipts	1 0 6		
		46 17 2	
			1128 8 9
Total Funds			£4961 8 4
Represented by—			
£3307, 5s. 6d. 2½% Guaranteed Stock (1933) at cost		£2816 18 1	
£1528, 0s. 4d. Local Loans 3% Stock at cost		1000 0 0	
£140, 9s. Royal Bank of Scotland Stock, taken over at 350%		491 11 6	
Due by Union Bank of Scotland, Ltd., on Deposit Receipt		652 18 9	
			£4961 8 4

Note.—Under the Will of the late Professor Charles Piazzi Smyth and his wife, the Society will, on the expiry of certain liferents, become entitled to payment of the residue to be applied as set out in the will.

EDINBURGH, 14*th October* 1938.—We have examined the preceding Accounts of the Treasurer of the Royal Society of Edinburgh for the Session 1937–1938, and have found them to be correct. The Investments held for the General Fund and the Prize Funds as shown in the foregoing Accounts have been verified by us as at 30th September 1938.

LINDSAY, JAMIESON & HALDANE, C.A.,
Auditors.

VOLUNTARY CONTRIBUTOR who has made a Single Payment under Law VI (end of para. 3).

Harry Richardson, Esq.	£10	10	0

VOLUNTARY CONTRIBUTORS under Law VI (end of para. 3), to 30th September 1938.

Sir James Barr	£1	1	0
Emeritus Professor F. O. Bower, F.R.S.	1	1	0
Principal O. C. Bradley	1	1	0
Dr G. S. Brock	1	1	0
Emeritus Professor E. W. W. Carlier	1	1	0
Professor E. G. Coker, F.R.S.	1	1	0
Emeritus Professor J. N. Collie, F.R.S.	1	1	0
L. MacQueen Douglas, Esq.	1	1	0
Dr Oswald Fergus	1	1	0
Dr R. A. Fleming	1	1	0
J. S. Ford, Esq., 1937–38, 1938–39	2	2	0
Alexander Fraser, Esq.	1	1	0
Dr W. F. Hume	1	1	0
Dr G. R. Jeffrey	1	1	0
Professor J. Graham Kerr, F.R.S.	1	1	0
Archibald King, Esq.	1	1	0
F. H. Lightbody, Esq.	1	1	0
Dr P. McBride, 1935–36 to 1937–38	3	3	0
	£22	1	0
Carried forward	£22	1	0
Dr George McGowan	1	1	0
Emeritus Professor J. MacKinnon	1	1	0
Principal D. Mallik	1	1	0
Dr H. R. Mill	1	1	0
Professor J. Miller	1	1	0
Dr A. Morgan	1	1	0
R. C. Mossman, Esq.	1	1	0
Professor Wm. Peddie	1	1	0
J. S. Pirie, Esq.	1	1	0
A. G. Ramage, Esq.	1	1	0
James Russell, Esq.	1	1	0
Edward Smart, Esq.	1	1	0
Charles A. Stevenson, Esq.	1	1	0
Dr H. F. Stockdale	1	1	0
G. Sutherland Thomson, Esq.	1	1	0
R. T. Thomson, Esq.	1	1	0
Very Rev. Dr L. MacLean Watt	1	1	0
Wm. Williamson, Esq.	1	1	0
Frank W. Young, Esq.	1	1	0
Total	£41	19	0

Single payment	£10	10	0
Other payments	41	19	0
Total	£52	9	0

THE COUNCIL OF THE SOCIETY.

24th October 1938.

President.

Professor Sir D'ARCY WENTWORTH THOMPSON, Kt., C.B., D.Litt., Hon. D.Sc., LL.D., F.R.S.

Vice-Presidents.

Professor F. A. E. CREW, M.D., D.Sc., Ph.D.
Lt.-Col. A. G. McKENDRICK, M.B., D.Sc., F.R.C.P.E.
Principal J. C. SMAIL, O.B.E., Companion Inst.E.E.
Professor JOHN WALTON, M.A., D.Sc.
JAMES WATT, W.S., LL.D.
Professor E. T. WHITTAKER, M.A., Hon. Sc.D., LL.D., F.R.S.

General Secretary.

Professor JAMES P. KENDALL, M.A., D.Sc., F.R.S.

Secretaries to Ordinary Meetings.

ALEXANDER C. AITKEN, M.A., D.Sc., F.R.S.
CHARLES H. O'DONOGHUE, D.Sc.

Treasurer.

E. MACLAGAN WEDDERBURN, O.B.E., LL.D., D.K.S.

Curator of Library and Museum.

LEONARD DOBBIN, Ph.D.

Councillors.

JOHN E. MACKENZIE, D.Sc.

Professor SYDNEY SMITH, M.D., F.R.C.P., D.P.H.

Emeritus Professor RALPH STOCKMAN, M.D., LL.D., F.R.C.P.E.

Professor LANCELOT T. HOGBEN, M.A., D.Sc., F.R.S.

Professor JAMES RITCHIE, M.A., D.Sc.

G. W. TYRRELL, A.R.C.S., D.Sc., F.G.S.

Emeritus Professor C. T. R. WILSON, C.H., M.A., D.Sc., LL.D., F.R.S.

Professor R. C. GARRY, M.B., Ch.B., D.Sc.

Professor R. J. D. GRAHAM, M.A., D.Sc.

Professor D. MURRAY LYON, M.D., F.R.C.P.E., D.P.H., D.Sc.

J. E. RICHEY, M.C., B.A., Sc.D., F.R.S., F.G.S.

The Hon. LORD ROBERTSON.

Office Staff.

Assistant Secretary and Librarian, G. A. STEWART.
Assistant Librarian, R. J. B. MUNRO.
Housekeeper, S. HEDDLE.

PATRON.

HIS MOST EXCELLENT MAJESTY THE KING.

FELLOWS OF THE SOCIETY,

Corrected to 24th October 1938.

N.B.—*Those marked* * *are Annual Contributors.*
,, ,, † *have commuted Voluntary Contribution* (*see 3rd Paragraph, Law VI*).

M-B. prefixed to a name indicates that the Fellow has received a Makdougall-Brisbane Medal.
K. ,, ,, ,, ,, Keith Medal.
N. ,, ,, ,, ,, Neill Medal.
V. J. ,, ,, ,, ,, the Gunning Victoria Jubilee Prize.
B. ,, ,, ,, ,, Bruce Medal.
B-P. ,, ,, ,, ,, Bruce-Preller Lectureship.
C. ,, ,, ,, has contributed one or more Communications to the Society's TRANSACTIONS or PROCEEDINGS.

Date of Election			Service on Council, etc.
1925	M-B. C.	* Aitken, Alexander Craig, M.A., D.Sc., F.R.S. (SECRETARY TO ORDINARY MEETINGS), Lecturer in Actuarial Science, University of Edinburgh (16 Chambers Street). 54 Braid Road, Edinburgh 10	1934–36. Sec. 1936–
1889		† Alison, John, M.A., LL.D., formerly Head Master, George Watson's College. 126 Craiglea Drive, Edinburgh 10	
1927	C.	* Allan, Douglas Alexander, D.Sc., Director, City of Liverpool Public Museums, William Brown Street, Liverpool	
1920	C. M-B.	* Allen, Herbert Stanley, M.A. (Cantab.), D.Sc. (London), F.R.S., Professor of Natural Philosophy, University of St Andrews	1921–24.
1938		* Anderson, Charles Henry William Gatacre, B.Sc. (Edin.), Headmaster and Superintendent, Royal Blind School, Edinburgh. 12 West Savile Road, Edinburgh 9	
1920	C. M-B.	* Anderson, Ernest Masson, M.A., D.Sc., F.G.S., 62 Greenbank Crescent, Edinburgh	
1905		Anderson, William, M.A., formerly Head Science Master, George Watson's College, Edinburgh. 6 Lockharton Crescent, Edinburgh 11	
1905		Andrew, George, C.B.E., M.A., B.A., H.M.I.S., (retired). Hamewith, Kilmacolm, Renfrewshire	
1930		* Annan, William, M.A., C.A., Professor of Accounting and Business Method, University of Edinburgh (South Bridge). Tofthill, Ferry Road West, Edinburgh 5	
1915		Anthony, Charles, M.Inst.C.E., M.Am.Soc.C.E., F.R.San.I., F.R.Met.S., F.R.A.S., F.C.S., Springcroft, Les Croutes, St Peter Port, Guernsey, Channel Islands	
1906		Appleton, Colonel Arthur Frederick, F.R.C.V.S. (*no permanent address until further notice*)	
1910	C.	Archibald, E. H., B.Sc., Professor of Chemistry, University of British Columbia, Vancouver, Canada	
1933		* Arnot, Frederick Latham, B.Sc. (Sydney), Ph.D. (Cantab.), Lecturer in Natural Philosophy, University of St Andrews. Yirdlag, Hepburn Gardens, St Andrews	
1921		* Arthur, William, M.A., Lecturer in Mathematics, University of Glasgow. 148 Carmunnock Road, Cathcart, Glasgow	
1938		* Bacsich, Paul, M.D. (Szeged, Hungary), Lecturer in Human Embryology, University of Glasgow. 81 Crown Road South, Glasgow, W. 2	
1920		* Bagnall, Richard Siddoway, Hon. D.Sc., F.R.E.S., 3 St Helen's Terrace, Low Fell, Co. Durham	
1920	C. N.	* Bailey, Edward Battersby, M.C., M.A., D.Sc. (Harvard), F.R.S., F.G.S., Director, Geological Survey of Great Britain and Museum of Practical Geology, Exhibition Road, London, S.W. 7	1932–35. V-P 1935–37.
1896	C.	† Baily, Francis Gibson, M.A., M.Inst.E.E., Emeritus Professor of Electrical Engineering, Heriot-Watt College, Edinburgh. Newbury, Juniper Green, Midlothian	1909–12, 1920–23. V-P 1929–32.

Date of Election			Service on Council, etc.
1934		* Bain, David, M.Sc. (Manch.), D.Sc. (Edin.), Lecturer in Technical Chemistry, University of Edinburgh (West Mains Road). 87 Cluny Gardens, Edinburgh 10	
1931	C.	* Bain, William Alexander, Ph.D., Reader in Pharmacology, School of Medicine, University of Leeds. 26 Weetwood Road, Headingley, Leeds 6	
1931		* Baird, Sir William Macdonald, Kt., J.P., Fellow and Past President of the Faculty of Surveyors of Scotland, F.S.A.Scot. Dalveen, Barnton Avenue, Davidson's Mains, Edinburgh 4	
1921		* Baker, Bevan Braithwaite, M.A., D.Sc., Professor of Mathematics, Royal Holloway College, Englefield Green, London	
1928	C.	* Baker, Edwin Arthur, D.Sc. (Edin.), Assistant at the Royal Observatory, Edinburgh. 17 Ladysmith Road, Edinburgh 9	
1905	C.	Balfour-Browne, William Alexander Francis, M.A., F.Z.S., F.L.S., F.R.E.S., F.R.M.S., Barrister-at-Law, formerly Professor of Entomology, Imperial College of Science, London. Hook Place, Burgess Hill, Sussex	
1933		* Banerjee, Prabodh Chandra, L.R.C.P.E., L.R.C.S.E., F.R.F.P.S.G., F.A.C.S., Major, I.M.S. C/o Lloyds Bank, Ltd., 101-1 Clive Street, Calcutta, India	
1938		* Bannerman, David Armitage, M.B.E., Sc.D., M.A. (Cantab.), Supernumerary Staff, Department of Zoology, British Museum (Nat. Hist.). 7 Pembroke Gardens, Kensington, London, W. 8	
1928		Barbour, George Brown, M.A. (Edin.), M.A. (Cantab.), Ph.D., F.G.S., Department of Geology, University of Cincinnati, Ohio, U.S.A.	
1886		Barclay, A. J. Gunion, M.A., 44A Belsize Park Gardens, Hampstead, London, N.W. 3	
1903		Bardswell, Noël Dean, M.V.O., M.D., M.R.C.P. (Edin. and Lond.) (no permanent address until further notice)	
1922		* Barger, George, M.A., D.Sc., Dr *h. c.* (Padua), Hon. D.Sc. (Liverp.), Hon. M.D. (Heidelberg), LL.D. (Michigan), F.R.S., Regius Professor of Chemistry, University of Glasgow, W. 2. 76 John Street, Helensburgh	1925-28.
1929		* Barker, Sydney George, O.B.E., D.I.C., F.Inst.P., Scientific Advisor, Indian Jute Mills Association. 191 Coombe Lane, Wimbledon, London, S.W. 20	
1914	C.	Barkla, Charles Glover, M.A., D.Sc., F.R.S., Professor of Natural Philosophy, University of Edinburgh (Drummond Street), Nobel Laureate, Physics, 1917. 4 Church Hill, Edinburgh 10	1915-18, 1924-27.
1937		* Barnett, Adam John Guilbert, B.Sc., Ph.D. (Edin.), Lecturer in Chemistry, Education Department, Lagos, Nigeria, B.W.A.	
1927		* Barnett, John, F.F.A., C.A., Scottish Widows' Fund Life Assurance Society, 9 St Andrew Square, Edinburgh 2	
1904		Barr, Sir James, C.B.E., M.D., LL.D., F.R.C.P., 16 Wildcroft Manor, Putney Heath, London, S.W. 15. (*Died, 16th November* 1938)	
1921		* Bartholomew, John, M.C., M.A., F.R.G.S., Geographical Institute, Duncan Street, Edinburgh. The Manor House, Inveresk	1925-28.
1927		* Bastow, Stephen Everard, M.Inst.E.E., M.Inst.Min.E. Northwood, Russell Place, Trinity, Edinburgh 5	
1929		* Bath, Frederick, Ph.D., Lecturer in Mathematics, University of Edinburgh (16 Chambers Street)	
1936		* Bayliss, Leonard Ernest, B.A., Ph.D., Lecturer in Biophysics, University of Edinburgh (Teviot Place). 52 Palmerston Place, Edinburgh 12	
1913		† Beard, Joseph, F.R.C.S.E., M.R.C.S., L.R.C.P., D.P.H. (Cantab.), formerly Medical Officer of Health, City of Carlisle. 8 Carlton Gardens, Carlisle	
1888		Beare, Sir Thomas Hudson, Kt., J.P., D.L., B.A., B.Sc., LL.D. (Edin.), M.Inst.C.E., Hon. M.I.Mech.E., Professor of Engineering, University of Edinburgh (Sanderson Engineering Laboratory, Mayfield Road). 10 Regent Terrace, Edinburgh 7	1907-09. V-P 1909-15, 1923-26.
1897	C.	Beattie, Sir John Carruthers, K.B., D.Sc., LL.D., formerly Vice-Chancellor and Principal, The University, Cape Town	
1893	C. M-B.	Becker, Ludwig, Ph.D., Emeritus Regius Professor of Astronomy, University of Glasgow. The Observatory, Dowanhill, Glasgow	
1933		* Begg, James Livingstone, F.G.S. (Treasurer, Geological Society of Glasgow). Elms, Mount Vernon, Glasgow	
1916		* Bell, Robert John Tainsh, M.A., D.Sc., LL.D. (Glas.), Professor of Mathematics, University of Otago, Dunedin, New Zealand	

Date of Election			Service on Council, etc.
1929		* Bennet, George, A.H.-W.C., B.Sc., A.M.I.Mech.E., Lecturer in Mechanical Engineering, Heriot-Watt College. 68 Arden Street, Edinburgh 10	
1936		Berry, John, M.A. (Cantab.), Ph.D. (St Andrews), Superintendent, Fisheries Research Station, University College, Southampton. Tayfield, Newport, Fife	
1893	C.	Berry, Sir George A., M.B., C.M., LL.D., F.R.C.S.E., King's Knoll, North Berwick	1916–19. V-P 1919–22.
1897	C.	Berry, Richard J. A., M.D., F.R.C.S.E., Director of Medical Services, Stoke Park Colony, Stapleton, Bristol. Rufford, Canford Lane, Westbury-on-Trym, Bristol	
1938		* Beveridge, Alexander William Morton, formerly Treasurer of the Bank of Scotland, and *ex officio* Chairman of the Managers of the Banks in Scotland. 44 Inverleith Place, Edinburgh 4	
1932		* Bhatia, Sohan Lal, M.C., M.A., M.D. (Cantab.), M.R.C.P., Major, I.M.S., Professor of Physiology and Dean, Grant Medical College, Bombay. Two Gables, Mount Pleasant Road, Malabar Hill, Bombay, India	
1937		* Biswas, Kalipada, M.A., D.Sc.(Edin.), Superintendent Royal Botanic Garden, Calcutta, India	
1937		* Blackie, Joseph John, Ph.D. (Edin.), F.C.S., F.I.C., a Partner in Messrs Duncan, Flockhart and Co., Chemical Manufacturers, 104 Holyrood Road, Edinburgh 8	
1936		* Blair, Duncan MacCallum, M.B., Ch.B. (Glas.), D.Sc. (Lond.), Regius Professor of Anatomy, University of Glasgow. 2 The University, Glasgow, W. 2	
1933		* Bolam, Thomas Robert, M.Sc. (Bristol), D.Sc. (Edin.), Lecturer in Chemistry, University of Edinburgh (West Mains Road). 8 Wilton Road, Edinburgh 9	
1915		* Boon, Alfred Archibald, D.Sc., B.A., F.I.C., Emeritus Professor of Chemistry, Heriot-Watt College, Ednburgh. 87 Warrender Park Road, Edinburgh 9	
1937	C.	* Born, Max, M.A. (Cantab.), Hon. D.Sc. (Bristol), Dr.phil. (Göttingen), Tait Professor of Natural Philosophy, University of Edinburgh (Drummond Street). 84 Grange Loan, Edinburgh 9	
1925		* Bose, Sahay Ram, M.A., D.Sc., F.L.S., Professor of Botany, Carmichael Medical College, Belgachia, Calcutta, India	
1886	C. N.	Bower, Frederick Orpen, M.A., D.Sc., LL.D., F.R.S., F.L.S., Emeritus Regius Professor of Botany, University of Glasgow. 2 The Crescent, Ripon, Yorks	1887–90, 1893–96, 1907–09, 1917–19. V-P 1910–16. P 1919–24.
1926		* Braid, Kenneth William, M.A. (Cantab.), B.Sc., Professor of Botany, West of Scotland Agricultural College, 6 Blythswood Square, Glasgow	
1907		† Bramwell, Edwin, M.D., LL.D., F.R.C.P. Edin. and Lond., formerly Professor of Clinical Medicine, University of Edinburgh. 23 Drumsheugh Gardens, Edinburgh 3	1935–38.
1932		* Brash, James Couper, M.C., M.A., M.B., Ch.B. (Edin.), M.D. (Birm.), Professor of Anatomy, University of Edinburgh (Teviot Place)	1932–35.
1918		* Bremner, Alexander, M.A., D.Sc., formerly Headmaster, Demonstration School, Training Centre, Aberdeen. 13 Belgrave Terrace, Aberdeen	
1893		Brock, G. Sandison, M.D., F.R.C.P.E., Greenbanks, St Saviour's, Jersey, C.I.	
1938		* Brook, Geoffrey Bernard, D.Sc. (Vet. Sci.), F.R.C.V.S., Health of Animals Division, Ministry of Agriculture, London, S.W. 1	
1937		* Brook, George Bernard, F.I.C., F.C.S., Chief Chemist to the British Aluminium Co., Ltd., London. The Auld Manse, Onich, Inverness-shire	
1934		* Brough, Patrick, M.A., B.Sc. (Glas.), D.Sc. (Sydney), Lecturer in Botany, University of Sydney, N.S.W.	
1907		Brown, Alexander, M.A., B.Sc., Professor of Applied Mathematics, University, Cape Town	
1936		* Brown, Andrew Johnstone, F.R.C.S., L.R.C.P., L.D.S. (Edin.), Lecturer on Metallurgy, Tutor in charge of Anæsthetic Department and Demonstrator in Radiology, Edinburgh Dental Hospital and School. 51 Minto Street, Edinburgh 9	

Date of Election			Service on Council, etc.
1937		* Brown, Archibald Gray Robertson, F.F.A., Manager and Actuary of the Life Association of Scotland. Barnshalloch, 30 Gillespie Road, Colinton Edinburgh 13	
1928		* Brown, Hugh Wylie, F.I.A., F.F.A., 1 Cobden Crescent, Edinburgh 9	
1924	C.	* Brown, Thomas Arnold, M.A., B.Sc., Professor of Mathematics, University College, Exeter	
1923		* Brown, Walter, M.A., B.Sc., Professor of Mathematics, University, Hong Kong, China	
1935		* Brownlie, James Law, M.D. (Glas.), D.P.H., M.R.C.P.E., formerly Chief Medical Officer, Department of Health for Scotland. C/o Mr Ross, Rannoch, 17 Ophir Road, Bournemouth, Hants	
1921		* Bruce, Alexander, B.Sc. (Edin.), Government Agricultural Chemist and City Analyst, The Laboratory, Turret Road S., Colombo, Ceylon	
1912		Bruce, Alexander Ninian, D.Sc., M.D., 8 Ainslie Place, Edinburgh 3	
1936		* Bruce, Sir Robert, Kt., D.L., J.P., LL.D., formerly Editor of the *Glasgow Herald*. Brisbane House, 9 Rowan Road, Glasgow, S. 1	
1898	C. K.	† Bryce, Thomas Hastie, M.A., M.D. (Edin.), LL.D., F.R.S., Emeritus Professor of Anatomy, University of Glasgow. The Loaning, Peebles	1911–14, 1922–25, 1935–38. V.P 1925–28.
1936		* Bryden, William, M.Sc., B.A., Ph.D. (Edin.), Union House, The University, Melbourne, S. Australia	
1917		* Burnside, George Barnhill, M.Inst.Mech.E., Fairhill, Dullatur	
1930	C.	* Burt, David Raitt Robertson, B.Sc. (St Andrews), F.L.S., Lecturer in Zoology, Ceylon University College, Colombo	
1896		Butters, John W., M.A., B.Sc., formerly Rector of Ardrossan Academy. 116 Comiston Drive, Edinburgh 10	
1929	C.	* Calder, Alexander, Ph.D., Chief Marketing Officer, Pig Marketing Board, Thames House, Millbank, London, S.W. 1	
1910		Calderwood, Rev. Robert Sibbald, D.D., formerly Minister of Cambuslang. 84 Findhorn Place, Edinburgh 9	
1893	C.	Calderwood, W. L., I.S.O., formerly Inspector of Salmon Fisheries of Scotland. Ardnacoille, Carr Bridge, Inverness-shire	1923–26.
1926	C. M-B.	* Cameron, Alfred Ernest, M.A., D.Sc. (Aberd.), Steven Lecturer in Agricultural and Forest Zoology, University of Edinburgh (10 George Square). 8 West Savile Road, Edinburgh 9	
1933		* Cameron, Finlay James, F.F.A., F.I.A., General Manager, Caledonian Insurance Company. Beech Knowe, Barnton, near Edinburgh	
1905	C.	Cameron, John, M.D., D.Sc., M.R.C.S., formerly Professor of Anatomy, Dalhousie University, Halifax, Nova Scotia. Balmashanner, Grove Road, East Cliff, Bournemouth	
1921		* Campbell, Andrew, Advisory Chemist, c/o Burmah Oil Co., Ltd., Research Laboratory, Fairlawn, Honor Oak Road, Forrest Hill, London, S.E. 30 Foxgrove Road, Beckenham, Kent	
1918		* Campbell, John Menzies, D.D.S. (Toronto), L.D.S. (Glas.), L.D.S. (Ontario), F.I.C.D., 14 Buckingham Terrace, Glasgow, W.	
1915	C. N.	* Campbell, Robert, M.A., D.Sc., F.G.S., Reader in Petrology, University of Edinburgh (Grant Institute of Geology, West Mains Road). Maryton, Colinton	1920–23.
1927	C.	* Cannon, Herbert Graham, M.A., Sc.D. (Cantab.), D.Sc. (Lond.), M.Sc. (Manc.), F.R.S., F.L.S., Beyer Professor of Zoology, University of Manchester. Hollin Knowle, Chapel-en-le-Frith, Derbyshire	
1899	C.	Carlier, Edmund W. W., B. ès Sc., M.Sc., M.D., F.R.E.S., Emeritus Professor of Physiology, University of Birmingham. Morningside, Dorridge, near Birmingham	
1938		* Carlow, Charles Augustus, Managing Director, Fife Coal Co., Ltd., President of the Institution of Mining Engineers. Linnwood Hall, Leven, Fife	
1910		Carnegie, Col. David, C.B.E., J.P., M.Inst.C.E., The Haven, Seasalter, Whitstable	
1931		* Carroll, John Anthony, M.A., Ph.D. (Cantab.), Professor of Natural Philosophy, University of Aberdeen. Marischal College, Aberdeen	
1905	C.	Carse, George Alexander, M.A., D.Sc., Reader in Natural Philosophy, University of Edinburgh (Drummond Street). 3 Middleby Street, Edinburgh 9	

Date of Election			Service on Council, etc.
1901			Carslaw, Horatio Scott, M.A., Sc.D. (Cantab.), D.Sc., LL.D. (Glas.), Emeritus Professor of Mathematics, University of Sydney, New South Wales. Burradoo, New South Wales	
1933		*	Carswell, John Irvine, B.Sc., Ph.D., A.M.Inst.C.E., A.M.Inst.Mech.E., Lecturer in Engineering, University of Edinburgh (Sanderson Engineering Laboratory, Mayfield Road). 43 Mansionhouse Road, Edinburgh 9	
1925		*	Carter, George Stuart, M.A., Ph.D., Corpus Christi College, Cambridge	
1932		*	Cathcart, Edward Provan, C.B.E., M.D., D.Sc., LL.D., F.R.S., Professor of Physiology, University of Glasgow. 28 Hillhead Street, Glasgow	
1932	C.	*	Childe, Vere Gordon, B.A., B.Litt., D.Litt. (Harvard), Hon. D.Sc. (Pennsylvania), F.R.A.I., F.S.A., Professor of Prehistoric Archæology, University of Edinburgh (14 Chambers Street)	
1925	C.	*	Chumley, James, M.A., Ph.D., formerly Lecturer in Oceanography, Department of Zoology, University of Glasgow. Thalassa, Milton Road East, Portobello, Midlothian	
1928	C.	*	Clark, Alfred Joseph, M.C., B.A., M.D., F.R.S., Professor of Materia Medica, University of Edinburgh (Teviot Place). 67 Braid Avenue, Edinburgh 10	1932–35.
1933		*	Clark, Arthur Melville, M.A. (Edin.), D. Phil. (Oxon.), Lecturer in English Literature, University of Edinburgh. 34 Bruntsfield Gardens, Edinburgh 10	
1891			Clark, John Brown, C.B.E., J.P., M.A., LL.D., formerly Head Master of George Heriot's School. Garleffin, 146 Craiglea Drive, Edinburgh 10	1928–1931. V-P 1931–34.
1935		*	Clark, Robert Selbie, M.A., D.Sc. (Aberd.), Scientific Superintendent, Fishery Board for Scotland. The Cottage, Murtle, Aberdeenshire	
1932		*	Clark, Sir Thomas, Bart., Publisher, Head of T. & T. Clark, Ltd. 6 Wester Coates Road, Edinburgh 12	
1909			Clayton, Thomas Morrison, M.D., D.Hy., B.Sc., D.P.H., Medical Officer of Health, Greenesfield House, Gateshead-on-Tyne	
1932		*	Clouston, David, C.I.E., M.A., B.Sc. (Agric.), D.Sc., formerly Director, Imperial Agricultural Research Institute, Pusa. Forthview, Boswall Road, Edinburgh 5	
1936	C.	*	Cockburn, Alexander Murray, Ph.D. (Edin.), Assistant, Geological Department, University of Edinburgh (Grant Institute of Geology, West Mains Road). 53 Ladysmith Road, Edinburgh 9	
1904	C.		Coker, Ernest George, M.A. (Cantab.), D.Sc. (Edin.), Hon. D.Sc. (Sydney and Louvain), M.Sc. (McGill), F.R.S., M.Inst.C.E., M.I.Mech.E., Emeritus Professor of Civil and Mechanical Engineering, University of London. Engineering Laboratories, 3 Farnley Road, Chingford, London, E. 4	
1904			Coles, Alfred Charles, M.D., D.Sc., York House, Poole Road, Bournemouth, W.	
1888	C. V. J.		Collie, John Norman, Ph.D., D.Sc., LL.D., F.R.S., F.C.S., F.I.C., Emeritus Professor of Organic Chemistry, University College, Gower Street, London. 20 Gower Street, London, W.C. 1	
1938		*	Colquhoun, Sir Iain, K.T., Baronet of Colquhoun and Luss, D.S.O., LL.D., Rector, University of Glasgow, 1934–37. Rossdu, Luss	
1909	C.		Comrie, Peter, M.A., B.Sc., LL.D., formerly Rector, Leith Academy. 19 Craighouse Terrace, Edinburgh 10	
1936		*	Cooper, The Rt. Hon. Thomas Mackay, O.B.E., K.C., M.P., M.A., LL.B., His Majesty's Advocate for Scotland. 7 Abercromby Place, Edinburgh 3	
1924	C.	*	Copson, Edward Thomas, M.A. (Oxon.), D.Sc. (Edin.), Professor of Mathematics, University College, Dundee (University of St Andrews). 14 Balmyle Road, Broughty Ferry, Dundee	
1937		*	Cousland, Charles Johnstone, formerly President, Royal Scottish Society of Arts. Achray, Kinnear Road, Edinburgh 4	
1928		*	Coutie, Rev. Alexander, B.Sc., Ph.D., Minister, Church of Scotland, Watten, Caithness	
1914			Coutts, William Barron, M.A., B.Sc., F.Inst.P., Assistant Professor of Fire Control Instruments, Military College of Science, Woolwich, S.E. 18. Craigmillar, 70 Cambridge Drive, London, S.E. 12	
1911			Cowan, Alexander, M.A. (Cantab.), Papermaker, Valleyfield, Penicuik, Midlothian	
1931		*	Cowan, John Macqueen, M.A., D.Sc. (Edin.), B.A. (Oxon.), F.L.S., Assistant Keeper, Royal Botanic Garden, Edinburgh. 17 Inverleith Place, Edinburgh 4	

Date of Election			Service on Council, etc.
1935		* Cowan, Samuel Hunter, Lt.-Col. R. E., Lecturer in Forestry Engineering, University of Edinburgh (George Square). New Club, Edinburgh 2	
1916	C.	† Craig, E. H. Cunningham, B.A. (Cantab.), Geologist and Mining Engineer, The Dutch House, Beaconsfield	
1908		Craig, James Ireland, M.A., B.A., 88 Sharia Kasr el Eini, Cairo, Egypt	
1925	C. K.	* Craig, Robert Meldrum, M.A., D.Sc., F.G.S., Lecturer in Economic Geology, University of Edinburgh (Grant Institute of Geology, West Mains Road)	
1937		* Craig, William Stuart McRae, B.Sc. (Glas.), M.D. (Edin.), F.R.C.P.E., Medical Officer, Ministry of Health, Whitehall, London, S.W. 1. Mellendean, Harriots Lane, Ashtead, Surrey	
1933		* Craig-Bennett, Arthur Lancelot, M.A., Ph.D. (Cantab.), Chief Fisheries Officer, Haifa, Palestine	
1903		† Crawford, Lawrence, M.A., D.Sc., Professor of Pure Mathematics, University, Cape Town	
1922	C.	* Crew, Francis Albert Eley, M.D., D.Sc., Ph.D. (Vice-President), Professor of Animal Genetics and Director of the Institute of Animal Genetics, University of Edinburgh (West Mains Road). 41 Mansionhouse Road, Edinburgh 9	1928–31. Sec. 1931–36. V-P 1936–
1931		* Crichton, John, M.A., B.Sc. (Edin.), 17 Willows Avenue, Morden, Surrey	
1936		* Cronshaw, Cecil John Turrell, B.Sc. (Vict.), Managing Director, Dyestuffs Group of Imperial Chemical Industries, Ltd. (including Scottish Dyes, Ltd.). Hexagon House, Blaikley, Manchester	
1929		* Cruickshank, Ernest William Henderson, M.D., D.Sc., Ph.D., Regius Professor of Physiology, University of Aberdeen	
1938		* Cruickshank, Martin Melvin, M.D., Ch.M. (Aberd.), F.R.C.S.E., D.O.M.S. (Lond.), Lieut.-Col. I.M.S., and Professor of Surgery, Madras Medical College. Pantheon House, Pantheon Road, Madras	
1914		Cumming, Alexander Charles, O.B.E., D.Sc., Red Latches, King's Drive, Caldy, Cheshire	
1928		* Cumming, William Murdoch, D.Sc. (Glas.), F.I.C., M.Inst.Chem.E., "Young" Professor of Technical Chemistry, Royal Technical College, Glasgow. Bonnieblink, 4 Newlands Road, Newlands, Glasgow, C. 1	
1917		* Cunningham, Brysson, D.Sc., B.E., M.Inst.C.E., Editor *The Dock and Harbour Authority*, formerly Lecturer in Waterways, Harbours, and Docks, University College, London. 141 Copers Cope Road, Beckenham, Kent	
1930		* Cunningham, John, C.I.E., B.A., M.D., Lt.-Colonel, I.M.S. (retired). South Bank, Grange Loan, Edinburgh 10	
1938		* Cursiter, Stanley, O.B.E., R.S.W., R.S.A., Director of National Galleries of Scotland, Brunstane House, Portobello, Midlothian	
1934		* Daly, Ivan de Burgh, M.A., M.D., B.Ch., Professor of Physiology, University of Edinburgh (Teviot Place). Cooliney, Spylaw Avenue, Edinburgh	1935–38.
1934		* Darling, Frank Fraser, Ph.D. (Edin.), N.D.A., Dundonnell, by Garve, Wester Ross	
1924	V. J.	* Darwin, Charles Galton, M.C., M.A., Sc.D., F.R.S., formerly Tait Professor of Natural Philosophy, University of Edinburgh, and Master of Christ's College, Cambridge. Director, National Physical Laboratory, Teddington, Middlesex Bushy Home, Teddington, Middlesex	1925–28. Sec. 1928–33. V-P 1933–36.
1935	C.	* Davidson, Charles Findlay, B.Sc. (St Andrews), F.G.S., Geologist, H.M. Geological Survey of Great Britain, Geological Survey and Museum, Exhibition Road, South Kensington, London, S.W. 7	
1932		* Davidson, Leybourne Stanley Patrick, B.A. (Cantab.), M.D. (Edin.), F.R.C.P.E., Professor of Medicine, University of Edinburgh (Teviot Place)	
1935		* Davidson, Maxwell, B.Sc. (Eng.), Ph.D., M.I.Mech.E., Lecturer in Heat Engines and Thermodynamics, University of Edinburgh (Sanderson Engineering Laboratory, Mayfield Road). 47 Liberton Drive, Edinburgh 9	
1930	C.	* Davies, Lewis Merson, M.A., F.G.S., F.R.A.I., Lt.-Colonel, Royal Artillery (retired). 8 Garscube Terrace, Murrayfield, Edinburgh 12	
1928		Dawson, Warren Royal, F.R.S.L., F.S.A., F.S.A.Scot., Honorary Librarian of Lloyd's, London, E.C. 3. Simpson House, Simpson, Bletchley, Bucks	
1923		* Deane, Arthur, M.R.I.A., Curator, Public Art Gallery and Museum, Belfast. Beach Road, Whitehead, Belfast	
1894		† Denny, Sir Archibald, Bart., LL.D., 5 St Helen's Place, London, E.C. 4	

Date of Election			Service on Council, etc.
1935	C.	* Desai, Bhimbhai Nichhabhai, B.A., M.Sc. (Bombay), D.Sc., Ph.D. (Edin.), Assistant Meteorologist, Government of India, Upper Air Observatory, Agra (U.P.), India	
1938		* Dewar, John Michael, M.D. (Edin.), M.R.C.P.E. 5 Chalmers Street, Edinburgh 3	
1937		* Dhar, Sasindra Chandra, D.Sc. (Edin.), Head of the Department of Mathematics, College of Science, Nagpur, C.P., India	
1924		* Dinham, C. H., B.A., H.M. Geological Survey. Edgemoor, 19 Highfield Road, Northwood, Middlesex	
1923		* Dixon, Ronald Audley Martineau, of Thearne, F.G.S., F.S.A.Scot., F.R.G.S., Thearne Hall, near Beverley	
1881	C.	Dobbin, Leonard, Ph.D. (CURATOR OF LIBRARY AND MUSEUM), formerly Reader in Chemistry, University of Edinburgh. Faladam, Blackshiels, Midlothian	1904–07, 1913–16. Curator 1934–
1918		* Dodd, Alexander Scott, Ph.D., F.I.C., F.C.S., City Analyst for Edinburgh. 20 Stafford Street, Edinburgh 3	
1925		* Donald, Alexander Graham, M.A., F.F.A., F.S.A.Scot., Secretary of the Scottish Provident Institution, Edinburgh. 18 Carlton Terrace, Edinburgh 7	
1937	C.	* Donald, Hugh Paterson, B.Sc., M.Agr.Sc. (N.Z.), Ph.D. (Edin.), Research Assistant, Institute of Animal Genetics, University of Edinburgh (West Mains Road)	
1882	C.	Dott, David B., F.I.C., Memb. Pharm. Soc., Ravenslea, Musselburgh	
1938		* Dott, Norman McOmish, F.R.C.S.E., Neurological Surgeon to the Royal Infirmary and the Lecturer on Neurological Surgery, University of Edinburgh. 3 Chalmers Crescent, Edinburgh 9	
1921	C. M-B.	* Dougall, John, M.A., D.Sc., 47 Airthrey Avenue, Glasgow, W. 4	
1901 & 1918		Douglas, Carstairs Cumming, M.D., D.Sc., Professor of Medical Jurisprudence and Hygiene, Anderson's College, Glasgow. Clonbeith, Milngavie, by Glasgow	
1910		Douglas, Loudon MacQueen, Newpark, Mid-Calder, Midlothian	
1934		* Dow, David Rutherford, M.D., D.P.H., F.R.C.P.E., Professor of Anatomy, University of St Andrews (University College, Dundee). 16 Windsor Street, Dundee	
1932		* Drennan, Alexander Murray, M.D. (Edin.), F.R.C.P.E., Professor of Pathology, University of Edinburgh (Teviot Place)	
1923	C.	* Drever, James, M.A., B.Sc., D.Phil., Professor of Psychology, University of Edinburgh (South Bridge). Ivybank, Wardie Road, Edinburgh 5	1929–32.
1901		Drinkwater, Thomas W., L.R.C.P.E., L.R.C.S.E., Chemical Laboratory, Surgeons' Hall, Edinburgh	
1923		* Drummond, J. Montagu F., M.A. (Cantab.), Harrison Professor of Botany, University of Manchester	1928–31.
1925		* Dryerre, Henry, M.R.C.S., Ph.D., Professor of Physiology, Royal (Dick) Veterinary College; Physiological Biochemist, Animal Diseases Research Association. Kenmore, Lasswade	
1921		* Drysdale, Charles Vickery, C.B., O.B.E., D.Sc. (Lond.), M.I.E.E., F.Inst.P., formerly Director of Scientific Research to the Admiralty. No. 151 Wick Hall, Furze Hill, Hove, Sussex	
1937		* Dunlop, Derrick Melville, B.A. (Oxon.), M.D. (Edin.), F.R.C.P.E., Christison Professor of Therapeutics, University of Edinburgh (Teviot Place). 1 Moray Place, Edinburgh 3	
1904		Dunlop, William Brown, M.A., 4A St Andrew Square, Edinburgh 2. Seton Castle, Longniddry, E. Lothian	
1933		* Dymond, Edmund Gilbert, M.A., Lecturer in Natural Philosophy, University of Edinburgh (Drummond Street). 7 Greenhill Gardens, Edinburgh 10	
1906	C.	Dyson, Sir Frank Watson, K.B.E., M.A., D.Sc., LL.D., F.R.S., formerly Astronomer Royal, Royal Observatory, Greenwich. 27 Westcombe Park Road, Blackheath, S.E. 3	
1934		* Edge, William Leonard, M.A., Sc.D. (Cantab.), Lecturer in Mathematics, University of Edinburgh (16 Chambers Street)	
1931		* Eggleton, Philip, D.Sc., Lecturer in Biochemistry, Department of Physiology, University of Edinburgh (Teviot Place)	

Date of Election			Service on Council, etc.
1924		* Elliot, Right Hon. Walter Elliot, P.C., M.C., M.B., Ch.B., D.Sc., LL.D., M.P., F.R.S., Minister of Health. 60 Eaton Square, London, S.W. 1	
1938		* Elphinstone, The Right Hon. Lord, K.T., LL.D., formerly President, Royal Scottish Geographical Society. Carberry Tower, Musselburgh, Midlothian	
1933		* Erskine, John Maxwell, General Manager of the Commercial Bank of Scotland, Ltd. Hazlieburn, West Linton	
1934		* Etherington, Ivor Malcolm Haddon, B.A. (Oxon.), Ph.D. (Edin.), Lecturer in Mathematics, University of Edinburgh (16 Chambers Street). 41 Scotland Street, Edinburgh 3	
1924		* Evans, Arthur Humble, M.A., Sc.D., Lecturer in English History. Cheviot House, Crowthorne, Berks	
1924		Evans, William Edgar, B.Sc., Assistant in charge of Herbarium, Royal Botanic Garden, Edinburgh 4	
1902		Ewen, John Taylor, O.B.E., J.P., B.Sc., M.I.Mech.E., H.M. Inspector of Schools (Emeritus), Pitscandly, Forfar	
1900	C.	Eyre, John William Henry, M.D., M.S. (Dunelm), D.P.H. (Cantab.), Emeritus Professor of Bacteriology, Guy's Hospital. 51 Portland Place, London, W.1	
1931		* Fairbairn, William Ronald Dodds, M.A., M.D., D.Psych. (Edin.), F.R.A.I. 18 Lansdowne Crescent, Edinburgh 12	
1936		* Fairweather, James Falconer, W.S., N.P., Fiscal of the Society of Writers to the Signet. 14 Henderland Road, Edinburgh 12	
1907	C.	Falconer, John Downie, M.A., D.Sc., F.G.S., formerly Director of the Geological Survey of Nigeria. The Cedars, Hatton Road, Harlington, Hayes, Middlesex	
1923		* Feldman, William Moses, M.D., B.S., F.R.C.P., F.R.A.S., Senior Physician, St Mary's Hospital for Women and Children, Plaistow. 851 Finchley Road, London, N.W. 11	
1928		* Fenton, Edward Wyllie, M.A., D.Sc. (Aberd.), F.L.S., Head of Botany Department, Edinburgh and East of Scotland College of Agriculture, 13 George Square, Edinburgh 8	
1907		Fergus, Edward Oswald, c/o Messrs M'Kay & Boyd, Solicitors, 50 Wellington Street, Glasgow	
1933		* Ferguson, Thomas, M.D., D.P.H. (Edin.), F.R.C.P.E., D.Sc., Medical Officer, Department of Health for Scotland. 4 Park Street, Falkirk	
1925	C.	* Ferrar, William Leonard, M.A., Fellow and Tutor of Hertford College, Oxford	
1932		* Findlay, Sir John Edmund Ritchie, Bart., B.A. (Oxon.), M.P., Proprietor of the *Scotsman*. Aberlour House, Aberlour, Banffshire	
1927	C.	* Finlay, Thomas Matthew, M.A., D.Sc. (Edin.), Lecturer in Palæontology, University of Edinburgh (Grant Institute of Geology, West Mains Road). 11 Dudley Terrace, Leith 6	
1911		† Fleming, John Arnold, F.C.S., Pottery Manufacturer, Locksley, Helensburgh, Dumbartonshire	
1906		*Fleming, Robert Alexander, M.A., M.D., LL.D., F.R.C.P.E., Consulting* Physician, Royal Infirmary. 10 Chester Street, Edinburgh 3	
1900	C. N.	Flett, Sir John S., K.B.E., M.A., D.Sc., LL.D., F.R.S., formerly Director of the Geological Survey of Great Britain and Museum of Practical Geology, Exhibition Road, South Kensington, London, S.W. 7	1916–19.
1892		Ford, John Simpson, F.I.C., 7 Corrennie Drive, Edinburgh 10	
1928	C.	* Forrest, James, M.A., B.Sc. (Glas.), D.Sc. (St Andrews), Lecturer in Physics, University College, Dundee. Cumbrae, Oxford Street, Blackness, Dundee	
1933		* Forrester, Charles, A.H.-W.C., Ph.D., F.I.C., F.Inst.F., Principal and Professor of Chemistry, Indian School of Mines, Dhanbad, India	
1920	C.	* Franklin, Thomas Bedford, B.A. (Cantab.), 28 Kingshill Drive, Kenton, Middlesex	
1910		Fraser, Alexander, Actuary, 5 St Margaret's Road, Edinburgh 9	
1909		* Fraser, David Kennedy, M.A., B.Sc., Psychologist to Glasgow Education Authority. Edge o' the Moor, Milngavie, Dumbartonshire	
1934		* Fraser, George, Chartered Civil Engineer, M.Inst.C.E., M.I.Struct.E. 25 Murrayfield Gardens, Edinburgh 12	
1928		* Fraser, Sir John, K.C.V.O., M.C., M.D., Ch.M., F.R.C.S.E., Regius Professor of Clinical Surgery, University of Edinburgh (Royal Infirmary). 20 Moray Place, Edinburgh 3	
1928		* Fraser, Kenneth, M.D. (Edin.), D.P.H. (Cantab.), D.T.M. (Edin.), County Medical Officer of Health, Cumberland. The Croft, Scotby, near Carlisle	

Date of Election			Service on Council, etc.
1914		Fraser, William, F.R.A.S., F.S.A.Scot., Managing Director, Neill & Co., Ltd., Printers, 212 Causewayside, Edinburgh 9	
1907		Galbraith, Alexander, Ravenswood, Dalmuir, Glasgow	
1933		* Galbraith, Augustus William de Rohan, M.Inst.C.E., M.Inst.C.E.I., F.S.E., City Engineer, Christchurch, New Zealand, Chairman of the Advisory Council of the New Zealand Standard Institute. The Spur, Sumner, New Zealand	
1901		Ganguli, Sanjiban, M.A., formerly Principal, Maharaja's College, and Director of Public Instruction, Jaipur State, Jaipur, India	
1933		* Gardner, Alfred Charles, M.Inst.C.E., M.Inst.Mech.E., M.Inst.E.E., F.G.S., Chief Engineer, Clyde Navigation Trust, 16 Robertson Street, Glasgow. 117 Fotheringay Road, Glasgow, S. 1	
1926		* Gardner, John Davidson, B.Sc., A.M.Inst.C.E., Partner, Gardner & Oswald, Civil Engineers, 84 George Street, Edinburgh 2	
1937		* Garry, Robert Campbell, M.B., Ch.B., D.Sc. (Glas.), Professor of Physiology, University College (University of St Andrews), Dundee. 58 Seafield Road, Broughty Ferry, Dundee	1938–
1930	C.	* Geddes, Alexander Ebenezer M'Lean, O.B.E., M.A., D.Sc., Lecturer in Natural Philosophy, University of Aberdeen. 12 Louisville Avenue, Aberdeen	
1909	C.	† Geddes, Rt. Hon. Sir Auckland Campbell, P.C., G.C.M.G., K.C.B., M.D., LL.D., Frensham, The Layne, Rolvenden Kent	
1909		† Gentle, William, B.Sc., Head Master, George Heriot's School. 10 West Savile Road, Edinburgh 9	
1914		Gibb, Sir Alexander, G.B.E., C.B., LL.D., F.R.S., M.Inst.C.E., Queen Anne's Lodge, Westminster, London, S.W. 1	
1910	C.	Gibb, David, M.A., B.Sc., Reader in Mathematics, University of Edinburgh (16 Chambers Street). 45 Fountainhall Road, Edinburgh 9	
1936		* Gibbons, Sydney Guy, Ph.D. (Lond.), Naturalist, Fishery Board for Scotland, Aberdeen. Dunmore, Milltimber, Aberdeenshire	
1917	C.	* Gibson, Alexander, M.B., Ch.B., F.R.C.S., 620 Medical Arts Building, Winnipeg, Canada	
1921		* Gibson, Walcot, D.Sc., F.R.S., F.G.S., formerly Assistant Director, H.M. Geological Survey (Scotland). Pathways, Fairlight Road, Hythe, Kent	
1911		Gidney, Sir Henry A. J., Kt., J.P., M.L.A., F.R.C.S.E., Lt.-Col., I.M.S. (retired), c/o The Allahabad Bank, Ltd., Calcutta, India	
1938		* Gifford, Charles Henry Pearson, M.A. (Cantab.), Partner in Baillie, Gifford & Co., 3 Glenfinlas Street, Edinburgh 3. 32 Stafford Street, Edinburgh 3	
1937		* Gilchrist, Andrew Rae, M.D. (Edin.), F.R.C.P.E., M.R.C.P., Assistant Physician, Royal Infirmary, Edinburgh, and Lecturer on Therapeutics, University of Edinburgh (Teviot Place). 6 Lansdowne Crescent, Edinburgh 12	
1933		* Gillespie, Robert Pollock, M.A., B.Sc., Ph.D. (Cantab.), Lecturer in Mathematics, University of Glasgow, 51 Clouston Street, Glasgow, N.W.	
1933		* Gillespie, Thomas Haining, Director-Secretary, Zoological Society of Scotland. Corstorphine Hill House, Murrayfield, Edinburgh 12	
1925		* Gillies, William King, M.A., B.A., F.E.I.S., LL.D. (Glas.), Rector of the Royal High School, Edinburgh. Davaar, 12 Suffolk Road, Edinburgh 9	
1909		Gladstone, Hugh Steuart, M.A., M.B.O.U., F.Z.S., Capenoch, Penpont, Dumfriesshire	
1911		Gladstone, Reginald John, M.D., F.R.C.S., Lecturer and Senior Demonstrator of Anatomy, King's College, University of London. 22 Court Lane Gardens, London, S.E. 21	
1934		* Glaister, John, M.D., D.Sc. (Glas.), Professor of Forensic Medicine, University of Glasgow. 5 Kew Terrace, Glasgow, W. 2	
1925	C.	* Goldie, Archibald Hayman Robertson, M.A., B.A., D.Sc., Superintendent, Meteorological Office, Air Ministry, Edinburgh. 6 Drumsheugh Gardens, Edinburgh 3	1929–32.
1901		Goodwillie, James, M.A., B.Sc., 239 Clifton Road, Aberdeen	
1938		* Gordon, Cecil, M.Sc. (Cape Town), Ph.D. (Lond.), Lecturer in Genetics, Department of Natural History, University of Aberdeen	
1938		* Gordon, William Smith, Ph.D., M.R.C.V.S., Chief Bacteriologist, Moredun Institute, Animal Diseases Research Association, Gilmerton. 2 Northfield, Liberton, Edinburgh	

Date of Election			Service on Council, etc.
1913	C. M-B.	Gordon, William Thomas, M.A., D.Sc. (Edin.), M.A. (Cantab.), Professor of Geology, University of London, King's College, Strand, W.C.	
1897		Gordon-Munn, John Gordon, M.D., Croys, Castle Douglas	
1934		* Gorrie, Robert Maclagan, D.Sc. (Edin.), Silviculturalist to Punjab Government. C/o Chief Conservator of Forests, Lahore, Punjab, India	
1938		* Goyal, Ram Kumar, M.B., B.S. (Punjab), M.R.C.P., M.R.C.S., Ph.D. (Edin.), Research Worker, School of Tropical Medicine, Calcutta, India	
1923		* Grabham, George Walter, O.B.E., M.A. (Cantab.), F.G.S., Government Geologist, Anglo-Egyptian Sudan. Box 178, Khartoum	
1924		Graham, Robert James Douglas, M.A., D.Sc., Professor of Botany, University of St Andrews	1938–
1931		* Grant, Robert, J.P., Publisher (Oliver & Boyd), Edinburgh. 6 Kilgraston Road, Edinburgh 10	
1935	C.	* Grant, Ronald, Ph.D. (Edin.), Department of Zoology, University of Chicago, Ill., U.S.A.	
1918		* Gray, William Forbes, F.S.A.Scot., 8 Mansionhouse Road, Edinburgh 9	
1937	C.	* Green, George, M.A., D.Sc. (Glas.), Lecturer in Applied Physics, University of Glasgow. 64 Partickhill Road, Glasgow, W. 1	
1938		* Greenlees, James Robertson Campbell, M.A., M.B., B.C. (Cantab.), Headmaster of Loretto School, Musselburgh	
1927	C. K.	* Greenwood, Alan William, D.Sc. (Melb.), Ph.D. (Edin.), Lecturer in the Institute of Animal Genetics, University of Edinburgh (West Mains Road)	
1922		* Greenwood, Rev. William Osborne, M.D. (Leeds), B.S. (Lond.), L.S.A., Clerk in Holy Orders, Woodroyd, 19 Ripon Road, Harrogate, Yorks	
1906		Greig, Edward David Wilson, C.I.E., M.D., D.Sc., Lt.-Col., I.M.S. (retired), 38 Coates Gardens, Edinburgh 12	
1931		* Greig, John Russell, Ph.D. (Edin.), Director, Moredun Institute, Animal Diseases Research Association. Wedderlie, Kirkbrae, Liberton 9	
1905		† Greig, Sir Robert Blyth, M.C., LL.D., formerly Secretary to the Department of Agriculture for Scotland. The Shaws, Barnton, Midlothian	1921–24. V-P 1924–27.
1935		* Grierson, Alexander Millar Meek, M.D. (Edin.), D.P.H. (Edin. and Glas.), Senior Assistant to the Medical Officer of Health, Public Health Department, Sunlight House, Manchester 3	
1910		Grimshaw, Percy Hall, I.S.O., F.R.E.S., formerly Keeper, Natural History Department, Royal Scottish Museum. 133 Liberton Brae, Edinburgh 9	
1899		† Guest, Edward Graham, J.P., M.A., B.Sc., 5 Newbattle Terrace, Edinburgh 10	
1927		* Gulland, John Masson, M.A. (Oxon.), D.Sc. (Edin.), Ph.D. (St Andrews), Sir Jesse Boot Professor of Chemistry, University College, Nottingham	
1907		Gulliver, Gilbert Henry, D.Sc., A.M.I.Mech.E., 99 Southwark Street, London, S.E.	
1930		* Guthrie, Douglas, M.D., F.R.C.S., Lecturer in Diseases of the Ear, Nose, and Throat, School of Medicine of the Royal Colleges, Edinburgh. 21 Clarendon Crescent, Edinburgh 4	
1933	C.	* Guthrie, William Gilmour, M.A. (Edin.), B.A. (Cantab.), Ph.D., Professor of Mathematics and Natural Philosophy, Magee College, Londonderry, Northern Ireland	
1911		Guy, William, F.R.C.S., L.R.C.P., L.D.S.Ed., LL.D. (Penn.), Consulting Dental Surgeon, Edinburgh Royal Infirmary; Lecturer on Human and Comparative Dental Anatomy and Physiology. 11 Wemyss Place, Edinburgh 3	
1934		* Haldane, David, B.Sc. (Edin.), Senior Geologist, H.M. Geological Survey (Scotland), 19 Grange Terrace, Edinburgh 9. 6 Kilmaurs Road, Edinburgh 9	
1936	C. N.	* Hamilton, William James, D.Sc. (Glas.), M.D., B.Ch. (Belfast), Professor of Anatomy, St Bartholomew's Hospital Medical College, London, E.C. 1	
1922		* Hannay, Robert Kerr, M.A., LL.D., H.R.S.A., Fraser Professor of Scottish History and Palæography, University of Edinburgh (South Bridge). Historiographer-Royal for Scotland. 5 Royal Terrace, Edinburgh 7	
1923		* Hanneford-Smith, William, A.M.Inst.C.E., Hon. A.R.I.B.A. 1 The Avenue, Gravesend, Kent	
1918		* Hardie, Patrick Sinclair, M.A., B.Sc., formerly Head of the Physics Department, Medical School, Cairo. 19 Ardmillan Terrace, Edinburgh 11	
1928		* Harding, William Gerald, F.R.Hist.S., F.S.A.Scot., F.R.E.S., Peckwater House, Charing, Kent	

Date of Election			Service on Council, etc.
1923	C.	* Harris, Robert Graham, M.A., D.Sc. (Edin.), 44 Manor Road, Farnborough, Hants	
1914		Harrison, Edward Philip, Ph.D., F.Inst.P., Chief Scientist, H.M.S. "Vernon," Portsmouth	
1934		Harrison, John Vernon, D.Sc.(Glas.), F.G.S., 34 Rowallan Gardens, Glasgow, W. 1	
1921		* Harrison, John William Heslop, D.Sc. (Durham), F.R.S., Professor of Botany and Reader in Genetics, King's College, Newcastle-upon-Tyne. The Avenue, Birtley, Co. Durham	
1926		* Harvey, William Frederick, C.I.E., M.A., M.B., C.M., D.P.H., Lieut.-Col., I.M.S. (retired), Histologist, Research Laboratory, Royal College of Physicians, Edinburgh. 56 Garscube Terrace, Edinburgh 12	
1936		* Henderson, David Kennedy, M.D., F.R.C.P.E., F.R.F.P.S.G., Professor of Psychiatry, University of Edinburgh. Tipperlinn House, Edinburgh 10	
1931		* Henderson, John, F.C.I.I., Manager and Secretary, Edinburgh Assurance Co., Ltd. Seaforth Cottage, York Road, Trinity, Edinburgh 5	
1936		* Henderson, Thomas, B.Sc. (Lond.), Secretary to the Educational Institute of Scotland. 2 Hillview Terrace, Edinburgh 12	
1929		* Henderson, Thomas, C.B.E., J.P., F.S.A.Scot., Actuary of the Savings Bank of Glasgow. 5 Belmont Crescent, Glasgow, W. 2	
1908		Henderson, William Dawson, M.A., B.Sc., Ph.D., Lecturer, Zoological Laboratories, University, Bristol. 77 Coldharbour Road, Bristol 6	
1937		* Hepburn, William Allan Forsyth, M.C., M.A., B.Ed. (Edin.), Director of Education, Ayrshire Education Authority. 2 St Leonard's Road, Ayr	
1925		* Heron, Alexander Macmillan, D.Sc. (Edin.), F.G.S., Director, Geological Survey of India, Calcutta, India	
1916		* Herring, Percy Theodore, M.D., F.R.C.P.E., Professor of Physiology, University of St Andrews. Linton, St Andrews	1917–20, 1931–34. V-P 1934–37.
1936		* Hewat, Andrew Fergus, M.D., F.R.C.P.E., Secretary, Royal College of Physicians, Edinburgh. 14 Chester Street, Edinburgh 3	
1922		Hindle, Edward, M.A., Sc.D. (Cantab.), Ph.D., A.R.C.S., Regius Professor of Zoology, University of Glasgow	
1904		Hobday, Sir Frederick T. G., Kt., C.M.G., Dr. Med. Vet. (Zurich), F.R.C.V.S., Hon. Veterinary Surgeon to H.M. the King, and Emeritus Professor of Surgery, Royal Veterinary College, London, N.W. 1. 31 Argyll Road, Kensington, London, W. 8	
1928	C.	* Hobson, Alfred Dennis, M.A. (Cantab.), Professor of Zoology, King's College, Newcastle-upon-Tyne	
1928		* Hodge, William Vallance Douglas, M.A. (Edin.), M.A. (Cantab.), F.R.S., Lowndean Professor of Astronomy and Geometry, University of Cambridge. 28 Barrow Road, Cambridge	
1938		* Hogarth, George, Chairman of the Fishery Board for Scotland, 101 George Street. 40 Elliot Road, Edinburgh 11	
1923	C. K.	* Hogben, Lancelot Thomas, M.A., D.Sc., F.R.S., Professor of Natural History, University of Aberdeen	1937–
1927		Holden, Henry Smith, D.Sc., F.L.S., Director of the East Midlands Forensic Science Laboratory, Burton Street, Nottingham	
1930		* Holland, Sir Thomas Henry, K.C.S.I., K.C.I.E., D.L., Hon. D.Sc., LL.D., F.R.S., Vice-Chancellor and Principal of the University of Edinburgh. Blackford Brae, Edinburgh 9	1931–32. V-P 1932–35.
1929	C.	* Hora, Sunder Lal, D.Sc. (Punjab et Edin.), F.L.S., F.Z.S., F.A.S.B., Senior Assistant Superintendent, Zoological Survey of India. Indian Museum, Calcutta	
1920	C.	* Horne, Alexander Robert, O.B.E., B.Sc., M.I.Mech.E., A.M.Inst.C.E., Professor of Mechanical Engineering, Heriot-Watt College, Edinburgh. 31 Queen's Crescent, Edinburgh 9	
1896		Horne, J. Fletcher, M.D., F.R.C.S.E., Shelley Hall, Huddersfield	
1912	C. M-B.	† Houstoun, Robert Alexander, M.A., Ph.D., D.Sc., F.Inst.P., Lecturer in Physical Optics, University of Glasgow. 45 Kirklee Road, Glasgow	1929–32.
1893		Howden, Robert, M.A., M.B., C.M., D.Sc., LL.D., Emeritus Professor of Anatomy, University of Durham. Dalruadh, Victoria Terrace, Crieff	

Date of Election			Service on Council, etc.
1933		* Hume, Edgar Erskine, D.S.M., M.A., M.D., LL.D., Lieut.-Col., U.S. Army, Librarian of the Army Medical Library, Washington. The Magnolias, Frankfort, Kentucky. *Temporary Address*, Medical Field Service School, Carlisle Barracks, Pa., U.S.A.	
1910		Hume, William Fraser, D.Sc. (Lond.), Director, Geological Survey of Egypt, Helwân, Egypt. The Laurels, Rustington, Sussex	
1927		* Hunt, Owen Duke, B.Sc. (Manch.), Corrofell, Newton Ferrers, South Devon	
1923		* Hunter, Rev. Adam Mitchell, M.A., D.Litt., Librarian of New College, Edinburgh. 3 Suffolk Road, Edinburgh 9	
1932		* Hunter, Andrew, M.A., B.Sc., M.B., Ch.B., F.R.S.C., F.R.F.P.S.G., Professor of Pathological Chemistry, University of Toronto, Canada	
1928		* Hunter, Arthur, F.F.A., LL.D. (Edin.), Chevalier de la Légion d'Honneur, Vice-President and Chief Actuary of the New York Life Insurance Co. 124 Lloyd Road, Montclair, N.J., U.S.A.	
1916		* Hunter, Charles Stewart, M.A., L.R.C.P.E., L.R.C.S.E., D.P.H., F.R.E.S., Cotswold, 36 Streatham Hill, London, S.W. 2	
1911		Hunter, Gilbert Macintyre, M.Inst.C.E., M.Inst.E.S., M.Inst.M.E., 27 Kilmaurs Road, Edinburgh 9	
1935		* Hutchinson, Arthur Cyril William, M.D.S. (Manch.), D.D.S. (Witwatersrand), Dean of the Edinburgh Dental Hospital and School. 12 Glencairn Crescent, Edinburgh 12	
1923	C.	* Ince, Edward Lindsay, M.A. (Cantab.), D.Sc. (Edin.), Lecturer in Technical Mathematics, University of Edinburgh (16 Chambers Street)	
1920		* Inglis, James Gall, Publisher. 36 Blacket Place, Edinburgh 9	
1927		* Inglis, John Alexander, of Auchindinny and Redhall, K.C., M.A. (Oxon.), LL.B. (Edin.), King's and Lord Treasurer's Remembrancer. 13 Randolph Crescent, Edinburgh 3	1935–38.
1912		Inglis, Robert John Mathieson, M.Inst.C.E., Chief Engineer, Southern Area, L.N.E.R. Dixton, Monken Hadley, Herts	
1936		* Innes, Donald Esme, M.C., M.A. (Oxon.), Professor of Geology, University of St Andrews. Cortina, St Andrews	
1917		* Irvine, Sir James Colquhoun, Kt., C.B.E., D.L., Ph.D. (Leipzig), D.Sc. (St Andrews), Hon. D.Sc. (Liverpool, Princeton), Hon. Sc.D. (Cantab., Yale, Pennsylvania), Hon. LL.D. (Glas., Aberd., Edin., and Toronto), Hon. D.C.L. (Durham), F.R.S., Hon. F.E.I.S., Vice-Chancellor and Principal of the University of St Andrews	1920–22. V-P 1922–25.
1930	C.	* Jack, David, M.A., B.Sc. (Edin.), Ph.D. (St Andrews), Lecturer in Natural Philosophy, United College, University of St Andrews. 22 Grange Road, St Andrews	
1923		* Jack, John Louttit, C.B.E., Solicitor, Deputy Secretary, Department of Health for Scotland, 121A Princes Street, Edinburgh 2	
1938		* Jamieson, James Dalgleish Hamilton, H.D.D., L.D.S.Ed., Lecturer on Dental Diseases, University of Edinburgh. 29 and 58 George Square, Edinburgh 8	
1912	C.	Jeffrey, George Rutherford, M.D. (Glas.), F.R.C.P.E., 11 Langlands Gardens, Hampstead, London, N.W. 3	
1934		* Jeffrey, Sir John, K.C.B., C.B.E., formerly Under-Secretary of State for Scotland. 9 Cluny Gardens, Edinburgh 10	
1906	C. K.	Jehu, Thomas John, M.A., M.D., F.G.S., Professor of Geology, University of Edinburgh (Grant Institute of Geology, West Mains Road). 35 Great King Street, Edinburgh 3	1917–20, 1923–26. V-P 1929–32.
1900		† Jerdan, David Smiles, M.A., D.Sc., Ph.D., Avenel, Melrose	
1895		Johnston, Col. Henry Halcro, C.B., C.B.E., D.Sc., M.D., C.M. (Edin.), F.L.S., late Administrative Staff, Army. C/o Messrs Glyn, Mills & Co., Holts Branch, Kirkland House, London, S.W. 1	
1936		* Johnston, John McQueen, M.D. (Glas.), F.R.C.S.E., Pharmacologist, Department of Health for Scotland. 18 Berkeley Terrace, Glasgow, C. 3	
1928		* Johnston-Saint, Percy Johnston, M.A. (Cantab.), Conservator, Wellcome Historical Medical Museum, 183–193 Euston Road, London, N.W. 1. 4 Wyndham Place, Bryanston Square, London, W. 1	
1928		* Johnstone, Robert William, C.B.E., M.A., M.D. (Edin.), F.R.C.S.E., M.R.C.P.E., Professor of Midwifery and Diseases of Women, University of Edinburgh. 26 Palmerston Place, Edinburgh 12	
1927		* Jones, Edward Taylor, D.Sc. (Lond.), Professor of Natural Philosophy, University of Glasgow	1927–30.

Date of Election			Service on Council, etc.
1928	C.	* Jones, Tudor Jenkyn, D.Sc., M.B., Ch.B. (Glas.), Lecturer in Anatomy (Embryology), University of Liverpool	
1922		* Juritz, Charles Frederick, M.A., D.Sc., F.I.C., Chief of the Union Department of Chemistry. Grenoble, Avenue Fresnaye, Sea Point, Cape Town, South Africa.	
1936		* Kemball, Charles Henry, H.D.D., L.D.S., D.D.S. (Univ. Pennsylvania), Dental Surgeon, Lecturer on Orthodontics in Edinburgh Dental Hospital and School. 20 Ainslie Place, Edinburgh 3	
1925	C.	* Kemp, Charles Norman, B.Sc., Technical Radiologist, Secretary of the Royal Scottish Society of Arts. Ivy Lodge, Laverockbank Road, Edinburgh 5	
1929	C.	* Kendall, James Pickering, M.A., D.Sc., F.R.S. (GENERAL SECRETARY), Professor of Chemistry, University of Edinburgh (West Mains Road). 14 Mayfield Gardens, Edinburgh 9	1931–33. Sec. 1933–36. Gen. Sec. 1936–
1912		† Kennedy, Robert Foster, M.D. (Belfast), M.B., B.Ch. (R.U.I.), Associate Professor of Neurology, Cornell University, New York. 410 East 57 Street, New York City, U.S.A.	
1927		* Kennedy, Walter Phillips, Ph.D. (Edin.), L.R.C.P. and S.E., A.I.C., Professor of Physiology, Royal College of Medicine, Baghdad, Iraq	
1935		* Kenneth, John Henry, M.A., Ph.D. (Edin.), Assistant, Imperial Bureau of Animal Genetics, University of Edinburgh (West Mains Road). University Union, Edinburgh 8	
1909		Kenwood, Henry Richard, C.M.G., M.B., C.M., Emeritus Chadwick Professor of Hygiene, University of London. Wadhurst, Queen's Road, Finsbury Park, London, N.	
1925	C. M-B.	* Kermack, William Ogilvy, M.A., D.Sc., LL.D., Chemist, Research Laboratory of the Royal College of Physicians, 2 Forrest Road, Edinburgh 1	
1903 & 1923	C. N.	Kerr, John Graham, M.A. (Cantab.), LL.D., F.R.S., Honorary Fellow of Christ's College, M.P., Scottish Universities, Emeritus Regius Professor of Zoology, University of Glasgow. Dalny Veed, Barley, near Royston, Herts	1904–07, 1913–16, 1924–27. V-P 1928–31.
1891		Kerr, Joshua Law, M.D., J.P. Stratford, Victoria, Australia	
1926		* Khastgir, Satis Ranjan, M.Sc. (Calcutta), D.Sc. (Edin.), Physics Department, University, Dacca, India	
1907		King, Archibald, M.A., B.Sc., H.M. Inspector of Schools, The Cottage, Barassie, Ayrshire	
1925		* King, Leonard Augustus Lucas, M.A., Professor of Zoology, West of Scotland Agricultural College, Glasgow. 14 Bank Street, Glasgow, W. 2	
1918		* Kingon, Rev. John Robert Lewis, M.A., D.Sc., The Manse, Simonston, Cape Colony, South Africa	
1937		* Kirby, Percival Robson, M.A., D.Litt., F.R.C.M., Professor of Music and Musical History, University of the Witwatersrand, Johannesburg, South Africa	
1937	C.	* Koller, Peo Charles, Ph.D. (Budapest), D.Sc. (Edin.), Cytologist, Institute of Animal Genetics, University of Edinburgh (West Mains Road). 49 George Square, Edinburgh 8	
1927		* Lambie, Charles George, M.C., M.D., F.R.C.P.E., Bosch Professor of Medicine, University of Sydney. Capri, 4 Wyuna Road, Point Piper, Sydney, N.S.W., Australia	
1920	C.	* Lamont, John Charles, Lieut.-Col., I.M.S. (retired), C.I.E., M.B., C.M. (Edin.), M.R.C.S., formerly Professor of Anatomy, Medical College, Lahore, India. 7 Merchiston Park, Edinburgh 10	
1925	C. N.	* Lang, William Henry, M.B., C.M., D.Sc., LL.D. (Glas.), F.R.S., Barker Professor of Cryptogamic Botany, University of Manchester	
1931		* Langrishe, John du Plessis, D.S.O., M.B., B.Ch. (Dub.), D.P.H., Lt.-Col. R.A.M.C. (retired), Lecturer in Public Health, University of Edinburgh (Usher Institute of Public Health, Warrender Park Road). 2 South Gillsland Road, Edinburgh 10	
1910	C.	Lauder, Alexander, D.Sc., formerly Head of Chemistry Department, Edinburgh and East of Scotland College of Agriculture, and Lecturer in Agricultural Chemistry, University of Edinburgh. 78 Dalkeith Road, Edinburgh 9	1917–20. Sec. 1923–28.

Date of Election			Service on Council, etc.
1885	C.	Laurie, Arthur Pillans, M.A., D.Sc., LL.D., formerly Principal, Heriot-Watt College, Edinburgh. 38 Springfield Road, St John's Wood, London, N.W. 8	1908–11, 1913–16.
1905		Lawson, David, M.A., M.D., L.R.C.P. and S.E., Druimdarroch, Banchory, Kincardineshire	
1903		Leighton, Gerald Rowley, O.B.E., M.D., D.Sc., formerly Medical Officer (Foods), Department of Health for Scotland. Sharston, near Ramsey, Isle of Man	
1937		* Leitch, William Orr, M.Inst.C.E., formerly Chief Engineer and General Manager Peking Mukden Railway. 1 Gordon Terrace, Edinburgh 9	
1930		* Lelean, Percy Samuel, C.B., C.M.G., F.R.C.S., L.R.C.P., D.P.H., Professor of Public Health, University of Edinburgh (Usher Institute of Public Health, Warrender Park Road). 4 South Lauder Road, Edinburgh 9	
1910		Levie, Alexander, F.R.C.V.S., D.V.S.M., Balmae, Manor Road, Littleover, Derby	
1916	C.	* Levy, Hyman, M.A., D.Sc., Professor of Mathematics, Imperial College of Science and Technology, London, S.W. 7	
1914	C. N.	Lewis, Francis John, D.Sc., F.L.S., Professor of Botany, Egyptian University, Abbissea, Cairo	
1918		* Lidstone, George James, F.F.A., F.I.A., LL.D., formerly Manager and Actuary, Scottish Widows' Fund Life Assurance Society. Hermiston House, Hermiston, Currie, Midlothian	1919–22.
1905		Lightbody, Forrest Hay, 53 Queen Street, Edinburgh 2	
1931		* Lightfoot, Nicholas Morpeth Hutchinson, M.A. (Cantab.), Lecturer in Mathematics, Heriot-Watt College, Edinburgh. 3 Park Gardens, Liberton, Edinburgh 9	
1923		* Lim, Robert Kho Seng, M.B., Ch.B., D.Sc., Peking Union Medical College, Department of Physiology, Peking, China	
1912		Lindsay, John George, M.A., B.Sc. (Edin.), Rector of Dunfermline High School	
1920	C.	* Lindsay, Thomas A., M.A., B.Sc., Head Master, Higher Grade School, Bucksburn, Aberdeenshire	
1912		Linlithgow, The Most Honourable the Marquis of, P.C., K.T., G.C.I.E., D.L., LL.D., Viceroy and Governor-General of India. Hopetoun House, South Queensferry	V-P 1934–37.
1903		† Liston, William Glen, C.I.E., M.D., Lt.-Col., I.M.S. (retired), Milburn Tower, Gogar, Corstorphine, Edinburgh 12	
1929		* Little, John Robert, F.C.I.I., F.C.I.S., formerly Manager and Secretary, Century Insurance Co., Ltd. 5 Dalrymple Crescent, Edinburgh 9	
1932		* Lockhart, James Balfour, M.A., B.Sc. (Edin.), Mathematical Master, Edinburgh Academy. Westering, Inverleith Grove, Edinburgh 4	
1926		* Lorraine, Norman Stanley Rees, M.D., D.P.H. (Edin. and Glas.), Medical Officer of Health, Benfleet Urban District. 1 Burlescoombe Leas, Burlescoombe Road, Thorpe Bay, Southend-on-Sea	
1930		* Low, James Wotherspoon, B.Sc., Ph.D., 1 Hamilton Park Avenue, Glasgow, W. 2	
1934		* Low, R. Cranston, M.D., F.R.C.P.E., formerly Lecturer in Dermatology, University of Edinburgh. 1 Randolph Crescent, Edinburgh 3	
1923	C.	* Ludlam, Ernest Bowman, M.A., D.Sc., Lecturer in Chemistry, University of Edinburgh (West Mains Road)	
1923		* Lyford-Pike, James, M.A., B.Sc., Lecturer in Forestry, University of Edinburgh. Rosetta, 56 Kirkbrae, Liberton, Edinburgh 9	
1924		* Lyon, David Murray, M.D., F.R.C.P.E., D.P.H., D.Sc., Professor of Clinical Medicine, University of Edinburgh (Royal Infirmary). Druim, Colinton, Edinburgh 11	1938–
1894		Mabbott, Walter John, M.A., formerly Rector of County High School, Duns, Berwickshire. The Hawthorn, Farnham Lane, Haslemere, Surrey	
1929		* M'Arthur, Donald Neil, D.Sc., F.I.C., Professor of Agricultural Chemistry, West of Scotland Agricultural College, Glasgow, C. 2. 35 Kersland Street, Glasgow, W. 2	
1921		* M'Arthur, Neil, M.A., B.Sc., Lecturer in Mathematics, University of Glasgow. The Whins, Heathfield Drive, Milngavie	
1926		* M'Bride, James Alexander, B.A. (Roy. Univ., Ireland), B.Sc. (Lond.), formerly Rector of Queen's Park Secondary School, Glasgow. Scottish Liberal Club, Princes Street, Edinburgh 2	

Date of Election			Service on Council, etc.
1883		M'Bride, Peter, M.D., F.R.C.P.E., 3 St Peter's Grove, York	
1931	C.	* McCallien, William John, D.Sc. (Glas.), Lecturer in Geology, University of Glasgow. 37 Partickhill Road, Glasgow, W. 1	
1935		* MacCallum, Peter, M.Sc., M.A. (New Zealand), M.B., Ch.B., D.P.H. (Edin.), Professor of Pathology, University of Melbourne. Blackrock House, Blackrock, Victoria, Australia	
1923		* M'Cracken, William, J.P., F.S.I., Englesea House, Crewe	
1931	C.	* M'Crea, William Hunter, M.A., Ph.D. (Cantab.), B.Sc. (Lond.), F.R.A.S., Professor of Mathematics, The Queen's University, Belfast. 61 Ulsterville Avenue, Belfast	
1918		* M'Culloch, Rev. James David, 3 Ardgowan Street, Greenock	
1920		* M'Donald, Stuart, M.A., M.D., F.R.C.P.E., Professor of Pathology, University of Durham. College of Medicine, Newcastle-upon-Tyne	
1928		* MacDonald, Thomas Logie, M.A., B.Sc. (Glas.), F.R.A.S., 1 Graingerville North, Newcastle-upon-Tyne 4	
1886		Macdonald, William J., M.A., 15 Comiston Drive, Edinburgh 10	
1931		* M'Dougall, John Bowes, M.D. (Glas.), F.R.F.P.S.G., F.R.C.P.E., Medical Director, British Legion Village, Preston Hall, Kent. Preston Hall, Aylesford, Kent	
1901	C.	MacDougall, R. Stewart, M.A., D.Sc., LL.D. (Edin.), Emeritus Professor of Biology, Royal (Dick) Veterinary College, Edinburgh. Ivy Lodge, Gullane, East Lothian	1914–17.
1910		Macewen, Hugh Allen, O.B.E., M.B., Ch.B., D.P.H. (Lond. and Cantab.), Local Government Board, Ministry of Health, Whitehall, London, S.W.	
1888	C.	M'Fadyean, Sir John, Kt., M.B., B.Sc., LL.D., formerly Principal and Professor of Comparative Pathology, Royal Veterinary College, Camden Town, London. Highlands House, Leatherhead	
1885	C.	† Macfarlane, John M., D.Sc., LL.D., Emeritus Professor of Botany. 427 West Hansberry Street, Germantown, Pa., U.S.A.	
1938		* MacGillivray, Allister Middleton, M.D. (St Andrews), Lecturer in Clinical Ophthalmology, University of St Andrews. 5 Clarendon Terrace, Dundee	
1897		MacGillivray of MacGillivray, Angus, M.D., C.M., D.Sc., LL.D., 23 South Tay Street, Dundee	
1878		M'Gowan, George, F.I.C., Ph.D., 21 Montpelier Road, Ealing, London, W. 5	
1932		* MacGregor, Archibald Gordon, M.C., D.Sc., Geologist, H.M. Geological Survey (Scotland). 1 Greenbank Terrace, Edinburgh 10	
1922		* Macgregor, Murray, M.A., D.Sc., F.G.S., Assistant Director (Scotland), H.M. Geological Survey, 19 Grange Terrace, Edinburgh 9	1930–33.
1903		M'Intosh, Donald C., M.A., D.Sc., formerly Education Officer, Elgin. Glenavon, Boat of Garten	
1911		M'Intosh, John William, M.R.C.V.S., Dollis Hill Farm, Cricklewood, London, N.W. 2	
1927	C.	* M'Intyre, Donald, M.B.E., M.D. (Glas.), F.R.C.S.E., Royal Samaritan Lecturer in Gynæcology, University of Glasgow. 9 Park Circus, Glasgow, C. 3	
1912	C.	M'Kendrick, Anderson Gray, M.B., D.Sc., F.R.C.P.E., Lt.-Col., I.M.S. (retired) (VICE-PRESIDENT), Superintendent, Research Laboratory, Royal College of Physicians, 2 Forrest Road, Edinburgh 1	1924–27. 1933–36. V.P 1936–
1914		M'Kendrick, Archibald, J.P., F.R.C.S.E., D.P.H., L.D.S., 12 Rothesay Place, Edinburgh 3	
1900	C.	M'Kendrick, John Soutar, M.D., F.R.F.P.S. (Glas.), 2 Buckingham Terrace, Hillhead, Glasgow	
1910	C.	Mackenzie, Alister, M.A., M.D., D.P.H., Principal Medical Officer and Lecturer in Hygiene, Training Centre, Jordanhill, Glasgow. 22 Queen's Gate, Dowanhill, Glasgow	
1916	C.	* Mackenzie, John E., D.Sc., Emeritus Reader in Chemistry, University of Edinburgh. 2 Ramsay Garden, Edinburgh 1	1936–
1938		* Mackie, Alexander, B.Sc., Ph.D. (Edin.), Science Master, Trinity Academy. 2 St John's Terrace, Edinburgh 12	
1929	C.	* Mackie, John, M.A., D.Sc., Rector, Leith Academy. 7 York Road, Trinity, Leith 5	
1928		* Mackie, Thomas Jones, M.D., M.R.C.P.E., Professor of Bacteriology, University of Edinburgh (Teviot Place). 22 Mortonhall Road, Edinburgh 9	

Date of Election			Service on Council, etc.
1936		* M'Kinlay, Peter Laird, M.D., D.P.H., Medical Officer (Statistics), Department of Health for Scotland. 69 Montrose Street, Clydebank	
1910		MacKinnon, James, M.A., Ph.D., LL.D., Emeritus Professor of Ecclesiastical History, University of Edinburgh. 12 Lygon Road, Edinburgh 9	1933–36.
1904		Mackintosh, Donald James, C.B., M.V.O., D.L., M.B., C.M., LL.D., Superintendent, Western Infirmary, Glasgow. 3 Kirklee Gardens, Glasgow, W. 2	
1899		Maclean, Sir Ewen John, J.P., D.L., M.D., D.Sc. (Hon.), LL.D., F.R.C.P. (Lond.), Emeritus Professor of Obstetrics and Gynæcology, Welsh National Medical School. 12 Park Place, Cardiff	
1933		* Macleod, James, F.I.C., Manager, Glasgow Corporation Chemical Works Department. 16 Colebrooke Street, Glasgow, W. 2	
1916	C.	* M'Lintock, William Francis Porter, D.Sc. (Edin.), Geological Survey and Museum, Exhibition Road, South Kensington, London, S.W. 7	
1936		* M'Michael, John, M.D., Ch.B., M.R.C.P., Johnston and Lawrence (Royal Society) Research Fellow in Medicine. 32 Mount Vernon Road, Edinburgh 9	
1923		* Macmillan, Rt. Hon. Lord, P.C., G.C.V.O., LL.D., 44 Millbank, Westminster, S.W. 1	
1938		* McMillan, William Hutchison, B.Sc. (Glas.), M.I.M.E., Hood Professor of Mining, University of Edinburgh, and Professor of Mining, Heriot-Watt College, Edinburgh. 5 Gordon Terrace, Edinburgh 9	
1932		* M'Neil, Charles, M.A., M.D. (Edin.), F.R.C.P.E., Professor of Child Life and Health, University of Edinburgh (Royal Edinburgh Hospital for Sick Children). 44 Heriot Row, Edinburgh 3	
1917		* Macpherson, Rev. Hector Copland, M.A., Ph.D., F.R.A.S., Guthrie Memorial U.F. Church. 7 Wardie Crescent, Edinburgh 5	
1921		* M'Quistan, Dougald Black, M.A., B.Sc., Associate-Professor of Natural Philosophy, Royal Technical College, Glasgow. 29 Viewpark Drive, Rutherglen	
1936		* McRae, William, C.I.E., M.A., D.Sc. (Edin.), Late Agricultural Adviser to the Government of India, and Director, Agricultural Research Institute, Pusa. Daramona, Gamekeepers' Road, Barnton, Midlothian	
1921	C.	* MacRobert, Thomas Murray, M.A., D.Sc., Professor of Mathematics, University of Glasgow. 10 The University, Glasgow	1931–34.
1921	C.	* M'Whan, John, M.A. (Glasgow), Ph.D. (Gött.), Lecturer in Mathematics, University of Glasgow. 37 Airthrey Avenue, Jordanhill, Glasgow, W. 4	
1927		* Madwar, Mohamed Reda, Ph.D. (Edin.), A.M.Inst.C.E., Director, Helwân Observatory, Egypt	
1898	C.	† Mahâlanobis, S. C., B.Sc. (Edin.), Professor of Physiology, University of Calcutta. P. 45 New Park Street, Calcutta	
1938		* Mainland, Donald, M.B., Ch.B., D.Sc. (Edin.), Professor of Anatomy, Forrest Building, *Dalhousie University, Halifax, Nova Scotia*	
1913		Majumdar, Tarak Nath, D.P.H. (Cal.), L.M.S., F.C.S., Professor of Hygiene, Carmichael Medical College, Belgachia, Calcutta	
1938		* Malcolm, Charles Alexander, M.A., Ph.D., Librarian, Signet Library. 21 Findhorn Place, Edinburgh 9	
1933		* Malcolm, John, M.D. (Edin.), Professor of Physiology, University of Dunedin, New Zealand, Medical School, King Street, Dunedin	
1908		Mallik, Devendranath, Sc.D., B.A., Principal, Carmichael College, Rungpur, Bengal, India	
1912		† Maloney, William Joseph, M.B.E., M.C., M.D. (Edin.), LL.D., formerly Professor of Neurology, Fordham University. Casa del Sale, Newport, Rhode Island, N.Y., U.S.A.	
1913		Marchant, Rev. Sir James, K.B.E., LL.D., F.R.A.S., F.L.S., Director, National Council for Promotion of Race-Regeneration. Pinegarth, Buccleuch Road, Bournemouth	
1901	C.	Marshall, Francis Hugh Adam, C.B.E., Sc.D., F.R.S., Reader in Agricultural Physiology, University of Cambridge. Christ's College, Cambridge	
1920	C.	* Marshall, John, M.A., D.Sc. (St Andrews), B.A. (Cantab.), University Reader in Mathematics, Bedford College, London. Logan House, 123 Torrington Park, London, N. 12	
1931		* Mason, John Huxley, F.R.C.V.S., Government Veterinary Laboratory, Onderstepoort, Pretoria, South Africa	
1913		Masson, George Henry, O.B.E., M.D., D.Sc., F.R.C.P.E., Carradale, Port of Spain, Trinidad, British West Indies	

Date of Election			Service on Council, etc.
1898	C. M-B.	Masterman, Arthur Thomas, M.A., D.Sc., F.R.S., formerly Superintending Inspector, H.M. Board of Agriculture and Fisheries. 3 Kedale Road, Seaford	1902–04.
1911		† Mathews, Gregory Macalister, M.B.O.U., Meadway, St Cross, Winchester, Hants	
1921		* Mathieson, John, F.R.S.G.S., Division Superintendent, Ordnance Survey (retired), 42 East Claremont Street, Edinburgh 7	
1906		Mathieson, Robert, F.C.S., St Serf's, Innerleithen	
1928		* Matthai, George, M.A. (Cantab.), Sc.D., F.Z.S., F.L.S., Professor of Zoology, Government College, Lahore, India	
1924		* Matthews, James Robert, M.A., F.L.S., Regius Professor of Botany, University of Aberdeen, and Keeper of the Cruickshank Botanic Garden	
1938		* Maxwell, Sir John Maxwell Stirling, K.T., of Pollok, Baronet, and of Corrour, D.L., LL.D. Pollok House, Glasgow, S. 3	
1932		* Maxwell, William, Managing Director of R. & R. Clark, Ltd. 14 South Inverleith Avenue, Edinburgh 4	
1917		* Maylard, A. Ernest, M.B., B.Sc. (Lond.), F.R.F.P.S. (Glasgow), Kingsmuir, Peebles	
1922		* Meakins, Jonathan Campbell, M.D., LL.D., F.R.C.P.E., Professor of Medicine and Director of the Department of Medicine, McGill University, Montreal, Canada	
1931		* Mears, Frank Charles, A.R.S.A., F.R.I.B.A., 44 Queen Street, Edinburgh 2	
1937	C.	* Melville, Harry Work, Ph.D. (Edin., Cantab.), D.Sc. (Edin.), Fellow of Trinity College, and Assistant Director, Colloid Science Laboratory, Cambridge	
1901	C.	Menzies, Alan W. C., M.A., Ph.D., F.C.S., Professor of Chemistry, Princeton University, Princeton, New Jersey, U.S.A.	
1927		* Menzies, Sir Frederick Norton Kay, K.B.E., M.D., LL.D. (Edin.), F.R.C.P.E., D.P.H. (Lond.), Medical Officer of Health and School Medical Officer, Administrative County of London, County Hall, London, S.E.	
1933	C.	* Menzies, William John Milne, Inspector of Salmon Fisheries of Scotland, Fishery Board for Scotland. Tighbeag, Whitehouse Road, Cramond Bridge, near Edinburgh	
1929		* Mercer, Walter, M.B., Ch.B., F.R.C.S.E., Lecturer in Clinical Surgery, University of Edinburgh (Royal Infirmary). 12 Rothesay Terrace, Edinburgh 3	
1917		* Merson, George Fowlie, Manufacturing Technical Chemist, St John's Hill Works, Edinburgh 8. 7 Cumin Place, Edinburgh 9	
1902	C.	† Metzler, William H., A.B., D.Sc., Ph.D., formerly Dean of the New York State College for Teachers, Albany, N.Y., U.S.A. 5003 South Salina Street, Syracuse, N.Y., U.S.A.	
1885	C. M-B.	Mill, Hugh Robert, D.Sc., LL.D., Hill Crest, Dormans Park, E. Grinstead	
1937		* Miller, James, R.S.A., F.R.I.B.A., Randolphfield, Stirling	
1910		Miller, John, M.A., D.Sc., formerly Professor of Mathematics, Royal Technical College. 212 Wilton Street, Glasgow, N.W.	
1936		* Miller, The Very Rev. John Harry, C.B.E., M.A., D.D., Principal of St Mary's College, University of St Andrews. St Mary's, St Andrews	
1930		* Miller, William Christopher, M.R.C.V.S., Courtauld Professor of Animal Husbandry, Royal Veterinary College, Camden Town, London, N.W. 1. Blair Hyrne, Hadley Common, Barnet, Herts	
1905		Milne, Archibald, M.A., D.Sc., Deputy Director of Studies, Edinburgh Provincial Training College. 38 Morningside Grove, Edinburgh 10	
1905		† Milne, C. H., M.A., D.Litt., formerly Head Master, Daniel Stewart's College. 19 Merchiston Gardens, Edinburgh 10	
1904	C.	Milne, James Robert, D.Sc., Lecturer in Natural Philosophy, University of Edinburgh (Drummond Street). 7 Grosvenor Crescent, Edinburgh 12	
1886		Milne, William, M.A., B.Sc., 70 Beechgrove Terrace, Aberdeen	
1933	C.	Milne-Thomson, Louis Melville, M.A. (Cantab.), F.R.A.S., Professor of Mathematics, Royal Naval College, Greenwich. Gothic House, Maze Hill, London, S.E. 10	
1899		Milroy, Thomas Hugh, M.D., B.Sc., LL.D., formerly Professor of Physiology, Queen's University, Belfast. Woodville, North Berwick	

Date of Election			Service on Council, etc.
1889	C. K.	Mitchell, A. Crichton, D.Sc., Hon. Doc. Sc. (Genève), formerly Director of Public Instruction in Travancore, India. 246 Ferry Road, Edinburgh 5. (Society's Representative on Governing Body of Heriot-Watt College)	1915–16, 1930–33. Cur. 1916–26. V-P 1926–29.
1897		† Mitchell, Sir George Arthur, Kt., D.L., J.P., M.A., LL.D., M.I.M.E., 9 Lowther Terrace, Kelvinside, Glasgow	
1900		Mitchell, James, M.A., B.Sc., Islay Lodge, Lochgilphead, Argyll	
1938		* Monteath, Harry Henderson, W.S., B.A., LL.B., Professor of Conveyancing, University of Edinburgh (South Bridge). 16 Palmerston Place, Edinburgh 12	
1936		* More, Francis, Chartered Accountant, of the firm of Lindsay, Jamieson and Haldane. 12 Albert Terrace, Edinburgh 10	
1896		Morgan, Alexander, O.B.E., M.A., D.Sc., LL.D., formerly Principal, Edinburgh Provincial Training College. 1 Midmar Gardens, Edinburgh 10	
1936		* Morgan, Daniel Owen, M.Sc. (Wales), Ph.D. (Lond.), Lecturer in Helminthology, Department of Zoology, University of Edinburgh (West Mains Road). 15 Mentone Terrace, Edinburgh 9	
1937		* Morison, John, C.I.E., M.B., Ch.B. (Glas.), D.P.H. (Cantab.), Lt.-Col. I.M.S. (retired). Engaged in Research in the Usher Institute of Public Health. 13 Cluny Drive, Edinburgh 10	
1926		* Morris, James Archibald, R.S.A., F.S.A.Scot., Savoy Croft, Ayr	
1919		* Morris, Robert Owen, O.B.E., M.A., M.D., C.M. (Edin.), D.P.H. (Liverpool). King Edward VII Welsh National Memorial Association (Tuberculosis). Hafod-ar-For, Aberdovey, N. Wales	
1892	C.	Morrison, J. T., M.A., D.Sc., Emeritus Professor of Mathematical Physics, University, Stellenbosch, South Africa	
1930		* Morton, Sir James, Kt., LL.D., Governing Director, Scottish Dyes, Ltd. Tuethur, Carlisle	
1901		Moses, O. St John, M.D., D.Sc., F.R.C.S., Lt.-Col., I.M.S. (retired), formerly Professor of Medical Jurisprudence, Medical College, Calcutta. 18 Manstone Road, Cricklewood, London, N.W. 2	
1892	C. K.	Mossman, Robert Cockburn, Lacar 4332, Villa Devoto F.C.P., Buenos Aires, Argentina	
1934		* Mowat, Magnus, C.B.E., T.D., M.Inst.C.E., M.I.Mech.E., Brigadier-General, Secretary of the Institution of Mechanical Engineers, Storey's Gate, London, S.W. 1	
1935	C.	* Mozley, Walter Alan, B.Sc. (Manitoba), Ph.D. (Edin.), Wandsworth Research Scholar, London School of Hygiene and Tropical Medicine, London, W.C. 1	
1916		* Muir, Sir Robert, Kt., M.A., M.D., Sc.D., LL.D., F.R.S., F.R.C.P.E., Emeritus Professor of Pathology, University of Glasgow. 30 Victoria Crescent Road, Glasgow, W. 2	
1935		* Munnoch, James, F.S.A.Scot., formerly Controller, General Post Office, Edinburgh. 15 Liberton Drive, Edinburgh 9	
1938	C.	* Munro, Sanford Sterling, B.S.A. (McGill), M.S. (Wisconsin), D.Sc. (Edin.), Poultry Geneticist, Dominion Department of Agriculture, Ottawa, Canada	
1933		* Murray, John, M.A. (Aberd.), Ph.D. (Edin.), Rector, The Academy, Annan. 9 Seaforth Avenue, Annan	
1932		* Murray, John Murdoch, B.Sc. (Edin.), Assistant Commissioner for Scotland, Forestry Commission. 76 Hillview Terrace, Corstorphine, Edinburgh 12	
1934		* Murray, Walter George Robertson, A.I.C., Technical Assistant, Department of Chemistry, University of Edinburgh (West Mains Road). 20 Montpelier Park, Edinburgh 10	
1935		* Narayana, Basudeva, M.Sc., M.B. (Calcutta), Ph.D. (Edin.), Professor of Physiology, University of Patna. Department of Physiology, Medical College, Patna, India	
1937		* Nasmith, Charles Roy, B.A., M.A. (Honorary), Colgate University, U.S.A., United States Consul in Edinburgh. Abden House, 1 Marchhall Crescent, Edinburgh 9	
1931		Nelson, Alexander, B.Sc. (Glas.), Ph.D. (Edin.), N.D.A., Lecturer in Plant Physiology and Agricultural Botany, University of Edinburgh. 14 Netherby Road, Edinburgh 5	

Date of Election			Service on Council, etc.
1924		* Nelson, Philip, M.A., M.D., Ph.D., F.S.A., Beechwood, Calderstones, Liverpool	
1898		Newman, Sir George, G.B.E., K.C.B., M.D., D.C.L., Hon. D.Sc., LL.D., F.R.C.P., formerly Chief Medical Officer, Ministry of Health and Board of Education. Grims Wood, Harrow Weald, Middlesex	
1928		* Nichols, James Edward, M.Sc. (Dunelm), Ph.D. (Edin.), Professor of Agriculture, University of Western Australia, Perth, W.A.	
1933	C.	* Nicol, Thomas, M.D., Ch.B., D.Sc. (Glas. and Lond.), F.R.C.S.E., Professor of Anatomy and Head of the Department of Anatomy, University of London, King's College, Strand, London, W.C. 2	
1927		* Noble, Thomas Paterson, M.D. (Edin.), F.R.C.S. Hillside, Ebbw Vale, Mon., Wales	
1934	C.	* Normand, Alexander Robert, M.A., B.Sc., Ph.D. (Edin.), formerly Professor of Chemistry, Wilson College, Bombay. 7 India Street, Edinburgh 3	
1928	C. N.	* O'Donoghue, Charles Henry, D.Sc. (Lond.) (SECRETARY TO ORDINARY MEETINGS), Reader in Zoology, University of Edinburgh (West Mains Road). Appin Lodge, Eskbank, Midlothian	Sec. 1936–
1925		* Ogg, William Gammie, M.A., Ph.D., Director, Macaulay Institute for Soil Research, Craigiebuckler, Aberdeen; Research Lecturer in Soil Science in the University of Aberdeen	
1923	C.	* Ogilvie, Alan G., O.B.E., M.A., B.Sc. (Oxon.), *Professor of Geography, University of Edinburgh* (High School Yards). 40 Fountainhall Road, Edinburgh 9	1932–35.
1929		* Ogilvie, Frederick Wolff, M.A. (Oxon.), LL.D. (Dublin), Director-General of the British Broadcasting Corporation. Broadcasting House, London, W. 1	
1886		Oliver, James, M.D., F.L.S., Physician to the London Hospital for Women. 123 Harley Street, London, W.	
1895	C.	† Oliver, Sir Thomas, Kt., D.L., M.D., LL.D., F.R.C.P., formerly Vice-Chancellor of the University of Durham. 7 Ellison Place, Newcastle-upon-Tyne	
1930		* Oliver, William, B.Sc., A.M.Inst.C.E., *Professor of Organisation of Industry and Commerce*, University of Edinburgh (South Bridge). 70 Netherby Road, Trinity, Edinburgh 5	
1930		* O'Riordan, George Francis, B.Sc. (Eng.), M.I.Mech.E., Principal of Battersea Polytechnic, London, S.W. 7. Hesslewood, 39 Langley Avenue, Surbiton, Surrey	
1924		* Orr, Sir John Boyd, Kt., D.S.O., M.C., M.A., D.Sc., M.D., LL.D., F.R.S., Director of the Rowett Research Institute for Research in Animal Nutrition, Aberdeen	
1915		* Orr, Lewis P., F.F.A., formerly General Manager of the Scottish Life Assurance Co., 3 Belgrave Place, Edinburgh 4	
1932		* Orr, Matthew Young, 38 Lennox Row, Edinburgh 5	
1908		Page, William Davidge, formerly of 13 Yarrell Mansions, Queen's Club Gardens, London, W. 14. (*Address not known*)	
1934		* Pal, Rudrendra Kumar, D.Sc. (Edin.), M.R.C.P.E., L.R.C.S.E., formerly Professor of Physiology, Prince of Wales Medical College, Patna. Nayasarak, Sylhet, Assam, India	
1905		Pallin, Colonel William Alfred, C.B.E., D.S.O., F.R.C.V.S., 5 Tower Gardens, Hythe, Kent	
1933		Parsons, Charles Wynford, M.A., Lecturer in Zoology, University of Glasgow. Mapledene, Ralston Road, Bearsden, Dumbartonshire	
1901		Paterson, David, Leewood, Rosslyn Castle, Midlothian	
1937		* Paterson, Thomas T., B.Sc. (Edin.), Fellow of Trinity College, Cambridge. Swanlea House, Buckhaven, Fife	
1936		* Paterson, William George Rogerson, B.Sc., Principal of the West of Scotland Agricultural College. Buckrigg, Beattock, Dumfriesshire	
1918		* Paterson, Very Rev. William Paterson, D.D., LL.D., Emeritus Professor of Divinity, University of Edinburgh (South Bridge). 17 South Oswald Road, Edinburgh 9	
1927		* Patterson, Charles, A.M.I.Mar.E., Lecturer in Mechanical Engineering Design, University of Edinburgh (Sanderson Engineering Laboratories, Mayfield Road). 22 Dudley Terrace, Trinity, Edinburgh 6	
1926		* Patton, Donald, M.A., B.Sc., Ph.D., Lecturer in Science, Glasgow Provincial College for the Training of Teachers. 15 Jordanhill Drive, Glasgow, W. 3	
1923	C.	* Peacock, Alexander David, D.Sc., Professor of Zoology, University College, Dundee	1935–38.

Date of Election			Service on Council, etc.
1914		Pearson, Joseph, D.Sc., F.L.S., formerly Director of the Colombo Museum, and Marine Biologist to the Ceylon Government. Director of the Tasmanian Museum, Hobart, Tasmania	
1904		Peck, Sir James Wallace, Kt., C.B., M.A., Secretary to the Scottish Education Department, 14 Queen Street, Edinburgh	1926–28.
1887	C. M·B.	Peddie, William, D.Sc., Professor of Natural Philosophy, University College, Dundee. The Weisha, Ninewells, Dundee	1904–07, 1908–11, 1933–36. V-P 1919–22.
1925		* Penman, David, C.I.E., D.Sc., M.Inst.M.E., Chief Inspector of Mines in India. St Agnes, Viewforth Street, Kirkcaldy	
1931	C.	* Phemister, James, M.A., D.Sc. (Glas.), Petrographer, H.M. Geological Survey and Museum, Exhibition Road, London, S.W. 7	
1938		* Phemister, Thomas Crawford, D.Sc. (Glas.), Ph.D. (Cantab.), F.G.S., Professor of Geology, University of Aberdeen	
1889		† Philip, Sir Robert William, Kt., M.A., M.D., LL.D., F.R.C.P.E., Professor of Tuberculosis, University of Edinburgh. 9 Palmerston Road, Edinburgh 9	V-P 1927–30.
1907	C.	† Phillips, Charles E. S., O.B.E., Castle House, Shooters Hill, Woolwich, S.E. 18	
1929	C.	* Phillips, John Frederick Vicars, D.Sc., F.L.S., Professor of Botany, University of the Witwatersrand, Johannesburg, Union of South Africa	
1935		* Pichamuthu, Charles Solomon, B.Sc. (Mysore), Ph.D. (Glas.), F.G.S., Assistant Professor of Geology, University of Mysore. Central College, Bangalore, India	
1932		* Pickard, James Nichol, B.A. (Cantab.), Ph.D. (Edin.), Lynburn, Carlops, Penicuik, Midlothian	
1928		* Pilcher, Robert Stuart, General Manager, Manchester Corporation Tramways. 55 Piccadilly, Manchester	
1908	C.	† Pirie, James Hunter Harvey, B.Sc., M.D., F.R.C.P.E., Research Pathologist and Bacteriologist, South African Institute for Medical Research. P.O. Box 1038, Johannesburg, South Africa	
1911		Pirie, James Simpson, M.Inst.C.E., 25 Grange Road, Edinburgh 9	
1906		Pitchford, Herbert Watkins, C.M.G., F.R.C.V.S., Victoria Club, Pietermaritzburg, South Africa	
1934		* Plenderleith, Harold James, M.C., B.Sc., Ph.D. (St Andrews), F.C.S., Deputy Keeper in Charge, Research Laboratory of British Museum, London. 198 Willesden Lane, London, N.W. 6	
1937		* Pollock, John Donald, O.B.E. (Mil.), D.L., M.D., Hon. D.Sc. (Oxon.), LL.D. (Edin.). Manor House, Boswall Road, Edinburgh 5	
1919		* Porritt, B. D., M.Sc. (Lond.), F.I.C., Director of Research, Research Association of British Rubber Manufacturers, 105 Lansdowne Road, Croydon, Surrey	
1888		† Prain, Sir David, Kt., C.M.G., C.I.E., M.A., M.B., LL.D., F.R.S., F.L.S., Lt.-Col., I.M.S. (retired), formerly Director, Royal Botanic Gardens, Kew, Surrey. The Well Farm, Warlingham, Surrey	
1937		* Prasad, Badri Narayan, Ph.D. (Edin.), M.Sc., M.B., D.T.M. (Cal.), Lecturer in Pharmacology, P. W. Medical College, Bankipore, P.O., Bihar, India	
1932		* Prasad, Gorakh, D.Sc. (Edin.), Reader in Mathematics, University of Allahabad. Beli Road, Allahabad, India	
1926	C.	* Prashad, Baini, D.Sc., Superintendent, Zoological Survey of India, Indian Museum, Calcutta	
1933		* Preston, Frank Anderson Baillie, L.R.I.B.A., F.S.A.Scot., Lecturer in Municipal Engineering, Royal Technical College, Glasgow. Craigrownie, Briarwell Road, Milngavie	
1915		† Price, Frederick William, M.D. (Edin.), Consulting Physician to the Royal Northern Hospital, London; Senior Physician to the National Hospital for Diseases of the Heart. 133 Harley Street, London, W.	
1932		* Price, Thomas Slater, O.B.E., D.Sc., (Lond., Birm.), Ph.D. (Leip.), F.R.S., Professor of Chemistry, Heriot-Watt College, Edinburgh. 2 Cluny Drive, Edinburgh 10	
1932		* Pringle, John, Hon. D.Sc., F.G.S., formerly Palæontologist, Geological Survey of Great Britain. 28 Bowen Road, Harrow, Middlesex	

Date of Election			Service on Council, etc.
1920	C.	* Purser, George Leslie, M.A. (Cantab.), F.Z.S., Lecturer in Embryology, University of Aberdeen	
1898		Purves, John Archibald, D.Sc., Chilliswood, Trull, Taunton	
1936	C.	* Raitt, Douglas Stewart, D.Sc., Ph.D. (Aberd.), F.L.S., Naturalist, Fishery Board for Scotland, Aberdeen. 41 Rosehill Drive, Aberdeen	
1899	C.	Ramage, Alexander G., Lochcote, Linlithgowshire	
1938		* Ramsay, Andrew Maitland, M.D., LL.D., F.R.F.P.S.G., formerly Lecturer in Ophthalmology, University of Glasgow. The Castle House, St Andrews	
1904		Ratcliffe, Joseph Riley, M.B., C.M., c/o The Librarian, University, Birmingham	
1900		Raw, Nathan, C.M.G., M.D., 22 Ashworth Road, Maida Vale, London, W. 9	
1937		Rawlins, Francis Ian Gregory, M.Sc. (Cantab.), F.Inst.P., Scientific Adviser to the Trustees of the National Gallery, London. 5 The Mount Square, Hampstead, London, N.W. 3	
1927	C.	* Read, Herbert Harold, D.Sc. (Lond.), A.R.C.S., F.G.S., formerly George Herdman Professor of Geology, University of Liverpool; Professor of Geology in the University of London Imperial College of Science and Technology, London, S.W. 7	
1929		* Read, Selwyn, B.A., Schoolmaster, Edinburgh Academy. Mackenzie House, Kinnear Road, Edinburgh 4	
1902		Rees-Roberts, John Vernon, M.D., D.Sc., D.P.H., 90 Fitzjohns Avenue, Hampstead, London, N.W. 3	
1913		Reid, Harry Avery, O.B.E., F.R.C.V.S., D.V.H., Veterinary Officer to the New Zealand Government. C/o High Commissioner for New Zealand, 415 Strand, London, W.C. 2	
1936		* Renouf, Louis Percy Watt, B.A. (Cantab.), M.Sc. (Nat. Univ. Ireland), Professor of Zoology, University College, Cork, Director of the University of Cork Biological Station. St Philomena's, Tivoli, Cork, I.F.S.	
1914		Renshaw, Graham, M.D., M.R.C.S., L.R.C.P., L.S.A., F.Z.S., Lecturer in Zoology, Extramural Department, University of Manchester. Editor of *Natureland*, Sale Bridge House, Sale, Manchester	
1913		† Richardson, Harry, O.B.E., M.C., M.Inst.E.E., M.Inst.M.E., 72 Oakwood Court, London, W. 14	
1908		Richardson, Linsdall, P.A.Inst.W.E. F.G.S. 104 Greenfield Road, Harbourne Birmingham	
1927		* Richey, James Ernest, M.C., B.A., B.A.I. (T.C.D.), Sc.D., F.R.S., F.G.S., District Geologist, H.M. Geological Survey (Scotland), 19 Grange Terrace, Edinburgh 9	1938–
1930		* Ritchie, Allan Watt, M.B.E., F.R.San.I., Chief Sanitary Inspector, City of Edinburgh. 2 Queensferry Terrace, Edinburgh 4	
1916	C.	* Ritchie, James, M.A., D.Sc., Professor of Natural History, University of Edinburgh. 31 Mortonhall Road, Edinburgh 9	1921–24, 1926–28, 1937– Sec. 1928–31. V-P 1931–34.
1914	C.	Ritchie, James Bonnyman, D.Sc., Rector, The Academy, Ayr. 28 Carrick Road, Ayr	
1937		* Ritchie, Mowbray, Ph.D., D.Sc. (Edin.), Lecturer in Chemistry, University of Edinburgh (West Mains Road)	
1906	C.	Ritchie, William Thomas, O.B.E., M.D., F.R.C.P. Edin. and Lond., formerly Professor of Medicine, University of Edinburgh (Teviot Place). 22 Alva Street, Edinburgh 2	
1936		* Robb, James, M.A., B.D., LL.B., LL.D. (St Andrews), Secretary to the Carnegie Trust for the Universities of Scotland. 26 Ormidale Terrace, Edinburgh 12	
1929	C.	* Robb, Richard Alexander, M.A., D.Sc., Lecturer in Mathematics, University of Glasgow. 27 Moor Road, Eaglesham, Renfrewshire	
1931		* Robb, William, N.D.A., Director of Research, Scottish Society for Research in Plant Breeding. Craigs House, Corstorphine, Edinburgh 12.	
1919		* Roberts, Alfred Henry, O.B.E., M.Inst.C.E., formerly Superintendent and Engineer, Leith Docks. Dohnavur, Ravelston Dykes, Edinburgh 4	
1926		* Roberts, John Alexander Fraser, M.A. (Cantab.), M.B., D.Sc., Stoke Park Colony, Stapleton, Bristol	

Date of Election			Service on Council, etc.
1928	C.	* Roberts, Owen Fiennes Temple, M.C., M.A. (Cantab.), Lecturer in Astronomy and Meteorology, University of Aberdeen. 20 Belgrave Terrace, Aberdeen	
1937		* Robertson, John Watson, M.A., B.Sc. (Aberd.), Headmaster, Central School, Aberdeen. 21 Belvedere Crescent, Aberdeen	
1937		* Robertson, Thomas Graham, The Hon. Lord Robertson, Senator of the College of Justice. 14 India Street, Edinburgh 3	1938–
1919		* Robertson, William Alexander, F.F.A., Century Insurance Co., Ltd., 18 Charlotte Square. Mardale, 3 Buckstone Park, Edinburgh 10	
1896	C.	Robertson, W. G. Aitchison, D.Sc., D.Litt., M.D., F.R.C.P.E., Barrister-at-Law, Lincoln's Inn. St Margarets, St Valerie Road, Bournemouth	
1932	C.	* Robson, John Michael, M.D., B.Sc., Lecturer in Materia Medica, University of Edinburgh (Teviot Place). 9 Golf Course Road, Bonnyrigg, Midlothian	
1926		* Romanis, William Hugh Cowie, M.A., M.B., M.C. (Cantab.), F.R.C.S., Surgeon to St Thomas's Hospital, London. 120 Harley Street, London, W. 1	
1916		* Ronald, David, M.Inst.C.E., formerly Chief Engineer, Scottish Board of Health, 125 George Street, Edinburgh 2	
1938		* Rosebery, The Right Hon. The Earl of, D.S.O., M.C., Lord Lieutenant of Midlothian. Dalmeny House, Edinburgh	
1909	C.	Ross, Alexander David, M.A., D.Sc., F.Inst.P., F.R.A.S., Professor of Physics, University of Western Australia, Perth, Western Australia	
1921		* Ross, Edward Burns, M.A., formerly Professor of Mathematics, Madras Christian College, Madras. 41 Liberton Brae, Edinburgh 9	
1935		* Rowatt, Thomas, M.I.Mech.E., F.S.A.Scot., Director, Royal Scottish Museum. Spottiswoode, Spylaw Bank Road, Colinton, Edinburgh	
1931	C. K	* Ruse, Harold Stanley, M.A. (Oxon.), D.Sc., Professor of Mathematics, University College, Southampton	
1906		Russell, Alexander Durie, B.Sc., F.R.A.S., formerly Head Mathematical Master, Falkirk High School. 12 Heugh Street, Falkirk	
1930		Russell, David, LL.D., Paper Manufacturer. Silverburn, Leven, Fife	
1902	C. K.	Russell, James, 22 Glenorchy Terrace, Edinburgh 9	
1937		* Russell, William Ritchie, M.D. (Edin.), F.R.C.P.E., M.R.C.P., Assistant Physician to the Royal Infirmary and to the Deaconess Hospital, Edinburgh. 8 Randolph Cliff, Edinburgh 3	
1934		* Rutherford, Daniel Edwin, M.A., B.Sc. (St Andrews), D.Math. (Amsterdam), Lecturer in Applied Mathematics, United College, University of St Andrews. 5 John Street, St Andrews	
1925	C.	* Saddler, William, M.A., B.A., Professor of Mathematics, Canterbury College, Christchurch, N.Z.	
1906		Saleeby, Caleb Williams, M.D., 13 Greville Place, Hampstead, London, N.W. 6	
1916	C.	* Salvesen, The Rt. Hon. Lord, P.C., K.C., LL.D., Judge of the Court of Session (retired), Dean Park House, Edinburgh 4	1920–22. V-P 1922–25.
1934		* Salvesen, Harold Keith, M.A. (Oxon. and Harvard), Captain (retired, I.A.), Shipowner, Inveralmond, Cramond, Midlothian	
1914		Salvesen, Colonel Theodore Émile (T.A.), of Culrain, F.R.S.A., F.S.A.Scot., Chevalier de la Légion d'Honneur. 37 Inverleith Place, Edinburgh 4	
1912	C. K.	Sampson, Ralph Allen, M.A., D.Sc., LL.D., F.R.S., formerly Astronomer Royal for Scotland and Professor of Astronomy, University of Edinburgh. Greenhill, 20 Observatory Road, Edinburgh 9	1912–15, 1919–21. V-P 1915–18, 1933–36. Sec. 1922–23. Gen. Sec. 1923–33.
1927	C.	* Sandeman, Ian, M.A., D.Sc., Ph.D. (St Andrews), Acting Chief Inspector of Schools, Education Department, Colombo, Ceylon	
1938		* Sandilands, James, A.H.-W.C., F.I.C., Senior Lecturer in Chemistry, Heriot-Watt College. 102 Westholmes Gardens, Musselburgh	
1930		* Sansome, Frederick Whalley, Ph.D., F.L.S., Senior Lecturer in Horticulture, Botany Department, University of Manchester	

Date of Election			Service on Council, etc.
1922		* Sarkar, Bijali Behari, M.Sc., D.Sc. (Edin.), Lecturer in Physiology, University, Calcutta. 33/3 Lansdowne Road, Calcutta	
1903		Sarolea, Charles, Ph.D., D.Litt., LL.D. (Montreal), formerly Professor of French, University of Edinburgh. 21 Royal Terrace, Edinburgh 7	
1935		* Say, Maurice George, Ph.D., M.Sc. (Lond.), M.I.E.E., Professor of Electrical Engineering, Heriot-Watt College, Edinburgh. Dreghorn Loan, Colinton, Edinburgh	
1927	C.	* Schlapp, Robert, M.A. (Edin.), Ph.D. (Cantab.), Lecturer in Applied Mathematics, University of Edinburgh (Drummond Street). 40A Morningside Park, Edinburgh 10	
1885	C.	† Scott, Alexander, M.A., D.Sc., F.R.S., formerly Director of Scientific Research at the British Museum. 117 Hamilton Terrace, London, N.W. 8	
1919		* Scott, Alexander, M.A., D.Sc., 3 Winton Terrace, Stoke-on-Trent	
1919		* Scott, Alexander Ritchie, B.Sc. (Edin.), D.Sc. (Lond.), Principal, London County Council, Beaufoy Institute, Prince's Road, London, S.E. 11	
1917		* Scott, Henry Harold, C.M.G., M.D., F.R.C.P., M.R.C.S., D.P.H., Director, Bureau of Hygiene and Tropical Diseases, Keppel Street, Gower Street, London, W.C. 1. 18 Ridgmount Gardens, Gower Street, London, W.C. 1	
1928		* Senior-White, Ronald, F.R.E.S., Malariologist, Bengal-Nagpur Railway, Kidderpore, P.O., Calcutta, India	
1930		* Shankland, Ernest Claud, F.R.Met.S., River Superintendent, Port of London Authority. Mariners, Balfour Gardens, Folkestone	
1927		* Sharpley, Forbes Wilmot, B.Sc. (Eng.) (Lond.), Ph.D., M.Inst.E.E., Professor of Electrical and Mechanical Engineering, Indian School of Mines, Dhanbad, India	
1931		* Shaw, John James M'Intosh, M.A., M.D., F.R.C.S., Lecturer in Surgery and Clinical Surgery, University of Edinburgh. Greenaway, Kinnear Road, Edinburgh 4	
1927		* Shearer, Ernest, M.A., B.Sc. (Edin.), Professor of Agriculture and Rural Economy, University of Edinburgh, and Principal, Edinburgh and East of Scotland College of Agriculture, 13 George Square, Edinburgh 8	
1931		* Shearer, James Fleming, M.A., B.Sc., Ph.D., Lecturer in Natural Philosophy, University of Glasgow. 149 Queen's Drive, Wavertree, Liverpool 15	
1932		* Simpson, Alexander Rudolf Barbour, B.Sc. (Edin.), M.A. (Cantab.), F.R.G.S., Hillstone School, Malvern, Worcestershire	
1908		Simpson, George Freeland Barbour, J.P., M.D., F.R.C.P.E., F.R.C.S.E., 43 Manor Place, Edinburgh 3	
1932	C.	* Simpson, John Baird, D.Sc. (Aberd.), Senior Geologist, H.M. Geological Survey (Scotland), 19 Grange Terrace, Edinburgh 9	
1938		* Sinclair, Arthur Henry Havens, M.D., F.R.C.S.E., Hon. Surgeon-Oculist to H.M. The King in Scotland, Consulting Ophthalmic Surgeon, Royal Infirmary, Edinburgh. 6 Charlotte Square, Edinburgh 2	
1900		Sinhjee, Sir Bhagvat, G.C.I.E., M.D., LL.D. (Edin.), H.H. the Thakur Sahib of Gondal, Kathiawar, Bombay, India	
1903		† Skinner, Robert Taylor, J.P., M.A., F.S.A.Scot., formerly House-Governor, Donaldson's Hospital. 35 Campbell Road, Edinburgh 12	
1937		* Slater, James Kirkwood, M.B. (Edin.), F.R.C.P.E., Assistant Physician, Royal Infirmary, Edinburgh, and Physician to the Deaconess Hospital, Edinburgh. 7 Walker Street, Edinburgh 3	
1930	C.	* Slater, Robert Henry, D.Sc., Ph.D. (Edin.), F.I.C., Department of Chemical Pathology, St Mary's Hospital, London, W. 2	
1929		* Smail, James Cameron, O.B.E., Companion Inst.E.E. (VICE-PRESIDENT), Principal, Heriot-Watt College, Edinburgh. 1 Grange Terrace, Edinburgh 9	1934-37. V-P 1937-
1926	C.	* Small, James, D.Sc., Professor of Botany, Queen's University, Belfast. Orkla, 50 Myrtlefield Park, Belfast	
1901		Smart, Edward, B.A., B.Sc., Tillyloss, Tullylumb Terrace, Perth	
1920		* Smellie, William Robert, M.A., D.Sc., Geologist on the Staff of the Anglo-Persian Oil Company. Baron Cliff, Cove, Dumbartonshire	
1937		* Smith, Alexander Martin, Ph.D., D.Sc. (Edin.), A.I.C., Lecturer in Agricultural Chemistry, University of Edinburgh, 13 George Square. 1 Mortonhall Road, Edinburgh 9	
1928		Smith, Alick Drummond Buchanan, M.A., B.Sc. (Agric.) (Aberd.), D.Sc. (Edin.), M.S.A. (Iowa), Lecturer, Institute of Animal Genetics, University of Edinburgh (West Mains Road)	

Date of Election			Service on Council, etc.
1937		* Smith, Horace George, B.Sc. (Glas.), Ph.D. (Bristol), Assistant, Department of Natural History, Marischal College, University of Aberdeen	
1921		* Smith, Norman Kemp, M.A., D.Phil., D.Litt., LL.D.. Professor of Logic and Metaphysics, University of Edinburgh (South Bridge). 14 Kilgraston Road, Edinburgh 9	
1923		* Smith, Percy James Lancelot, M.A. (Oxon.), F.I.C., F.C.S., Science Master, Loretto School. 47 Dalrymple Loan, Musselburgh	
1911		Smith, Stephen, B.Sc., 34 Craigmillar Park, Edinburgh 9	
1929		* Smith, Sydney, M.D., F.R.C.P., D.P.H., Professor of Forensic Medicine, University of Edinburgh (Teviot Place). 10 Oswald Road, Edinburgh 9	1936–
1919		* Smith, Sir William Wright, Kt., M.A., D. ès Sc., Regius Professor of Botany, University of Edinburgh, Regius Keeper of the Royal Botanic Garden, and King's Botanist in Scotland. Inverleith House, Edinburgh 4	Sec. 1923–28. V-P 1928–31.
1932		* Sneeden, Jean-Baptiste Octave, B.Sc., Ph.D. (Glas.), Lecturer on Heat Engines, Royal Technical College, Glasgow. 39 Kingshouse Avenue, Glasgow, S. 4	
1899		Snell, Ernest Hugh, M.D., B.Sc., D.P.H. (Cantab.), Barrister-at-Law, formerly Medical Officer of Health, Coventry. 3 Eaton Road, Coventry	
1933		* Somerville, John Livingston, C.A., Auditor, University of Edinburgh. 8 Ravelston Park, Edinburgh 4	
1929		* Southwell, Thomas, D.Sc., A.R.C.S., Walter Myers Lecturer in Parasitology, School of Tropical Medicine, University of Liverpool. 53 Greenhill Road, Mossley Hill, Liverpool 18	
1925		* Staig, Robert Arnot, M.A., Ph.D., Lecturer in Zoology, University of Glasgow. Glenlea, Lasswade, Midlothian	
1891		Stanfield, Richard, A.R.S.M., M.Inst.C.E., Emeritus Professor of Mechanics and Engineering, Heriot-Watt College, Edinburgh. 24 Mayfield Gardens, Edinburgh 9	1926–29.
1923		* Stebbing, Edward Percy, M.A., Professor of Forestry, University of Edinburgh (George Square)	
1923		* Stenhouse, Andrew G., F.G.S., 191 Newhaven Road, Edinburgh 6	
1929	C.	* Stephen, Alexander Charles, D.Sc., Keeper, Natural History Department, Royal Scottish Museum, Edinburgh. Eastcroft, Cramond Bridge, Edinburgh 4	
1910		Stephenson, Thomas, D.Sc., F.C.S., 65 Castle Street, Edinburgh 2. (*Died, 29th October* 1938)	
1931		* Steven, George Alexander, B.Sc. (Edin.), Assistant Naturalist, Marine Laboratory, Plymouth. 1 Seaview Villas, Pentyre Terrace, Plymouth, Devon	
1937	C.	* Steven, Henry Marshall, B.Sc., Ph.D. (Edin.), M.A., Hon. Causa (Oxon.), Professor of Forestry, University of Aberdeen. 75 Fountainhall Road, Aberdeen	
1886	C.	Stevenson, Charles A., B.Sc., M.Inst.C.E., Radella, North Berwick	
1919		* Stevenson, David Alan, B.Sc., M.Inst.C.E., 22 Glencairn Crescent, Edinburgh 12	
1935		* Stevenson, Eric, B.Sc. (Edin.), A.M.I.Mech.E., Lecturer in Engineering, University of Edinburgh (Sanderson Engineering Laboratory, Mayfield Road). 7 Beauchamp Road, Edinburgh 9	
1936		* Stewart, Alexander Dron, C.I.E., M.B., Ch.B. (Edin.), F.R.C.S.E., Lt.-Col. I.M.S. (retired), Superintendent of the Royal Infirmary, Edinburgh. Meadow Walk House, Edinburgh 3	
1931		* Stewart, Corbet Page, Ph.D.(Edin.), Lecturer in General Biochemistry, University of Edinburgh (Teviot Place). 17 Orchard Road South, Edinburgh 4	
1925		* Stewart, David Smith, Ph.D., M.Inst.C.E., Lecturer on Structural Engineering Drawing, University of Edinburgh (Sanderson Engineering Laboratory, Mayfield Road). 82 Lasswade Road, Edinburgh 9	
1938		* Stewart, James, M.A., D.Sc., Ph.D., Chief Biochemist, Moredun Institute, Animal Diseases Research Association, Gilmerton. 33 Hatton Place, Edinburgh 9	
1938		* Stewart, John Livingstone, B.Sc. (Edin.), M.R.C.V.S., Director of Veterinary Services, Gold Coast, Department of Animal Health, Pong-Tamale. P.O. Box No. 32, Tamale, Northern Territories, Gold Coast	
1924		* Stiles, Sir Harold Jalland, K.B.E., Kt., M.B., F.R.C.S.E., D.Sc. (Hon.), LL.D., Emeritus Professor of Clinical Surgery, University of Edinburgh. Whatton Lodge, Gullane, E. Lothian	1934–37.

Date of Election			Service on Council, etc.
1902		Stockdale, Herbert Fitton, LL.D., formerly Director of the Royal Technical College, Glasgow. Clairinch, Upper Helensburgh, Dumbartonshire	
1889	C.	Stockman, Ralph, M.D., LL.D., F.R.C.P.E., F.F.P.S.G., Emeritus Professor of Materia Medica and Therapeutics, University of Glasgow. White Lodge, Barnton Avenue, Edinburgh 4	1903–05, 1936–
1926		* Stokoe, William Norman, B.Sc., Ph.D. (Lond.), *Chief Chemist, Craigmillar* Creamery Co., Ltd. 8 Cobden Road, Edinburgh 9	
1906		Story, Fraser, O.B.E., formerly Professor of Forestry, University College, Bangor, North Wales. The Wall House, Yorke Road, Reigate, Surrey	
1907		Strong, John, C.B.E., M.A., LL.D., Emeritus Professor of Education, University of Leeds. C/o The Librarian, The University, Leeds	
1930	C.	* Stump, Claude Witherington, M.D., D.Sc., Professor of Embryology and Histology, University of Sydney	
1937		* Suffolk and Berkshire, The Rt. Hon. The Earl of, Glencairn, Eskbank, Midlothian	
1903		Sutherland, David W., C.I.E., M.D., M.R.C.P., Lt.-Col., I.M.S. (retired), Braeside, Belhaven, Dunbar	
1935		* Sutherland, John Derg, B.Sc., B.Ed., Ph.D. (Edin.), M.B., Ch.B., Lecturer in Psychology, University of Edinburgh. 2 Windsor Street, Edinburgh 7	
1930		* Sutherland, Sir John Donald, C.B.E., LL.D., Legion of Honour (France), Order of Leopold (Belgium), formerly Forestry Commissioner, Scotland. 11 Inverleith Row, Edinburgh 4	
1925		Sutton, Richard L., M.D., D.Sc., LL.D., 1308 Bryant Building, 1102 Grand Avenue, Kansas City, Mo., U.S.A.	
1932		* Swinton, William Elgin, B.Sc., Ph.D. (Glas.), F.L.S., F.Z.S., F.G.S., Curator of Fossil Reptiles and Amphibia, British Museum (Natural History), South Kensington, London, S.W.7	
1933		* Tait, John Barclay, B.Sc. (Edin.), Ph.D., A.H.-W.C., Senior Naturalist (Hydrographer), Marine Laboratory, Fishery Board for Scotland, Aberdeen. 23 Cromwell Road, Aberdeen	
1937		* Tait, John Guthrie, Scholar of Peterhouse College, Cambridge, B.A. (Cantab.), Barrister-at-Law, Lincoln's Inn, Hon. Fellow, Madras University, formerly Principal, Central College, Bangalore, India. 38 George Square, Edinburgh 8	
1890	C.	† Tanakadate, Aikitu, Hon. Professor of Natural Philosophy, Imperial University of Japan. Koisikawa, Zôsigayamati, 144, Tokyo, Japan	
1899		Taylor, James, M.A., formerly Mathematical Master, Edinburgh Academy. 18 Hillview, Blackhall, Edinburgh 4	
1933		* Taylor, George, D.Sc. (Edin.), F.L.S., Assistant Keeper, Department of Botany, British Museum. Ballochmyle, Loudwater, Rickmansworth, Herts	
1885	C.	Thompson, Sir D'Arcy Wentworth, Kt., C.B., M.A., LL.D. (Aberd., Edin.), Hon. D.Sc. (Dublin, Witwatersrand), D.Litt., F.R.S. (PRESIDENT), Professor of Natural History, University, St Andrews. 44 South Street, St Andrews	1892–95, 1896–99, 1907–10, 1912–15, 1922–25. V-P 1916–19. Curator 1926–34. P 1934–
1932		Thompson, Harold William, D.Litt. (Edin.), A.M., Ph.D. (Harvard), F.S.A. Scot., Professor of English, N.Y. State College, Albany, N.Y., U.S.A.	
1917	C. N.	* Thompson, John M'Lean, M.A., D.Sc., F.L.S., Professor of Botany, University of Liverpool	
1938		* Thomson, Arthur Landsborough, C.B., O.B.E., M.A., D.Sc. (Aberd.), Principal Assistant Secretary, Medical Research Council. 16 Tregunter Road, London, S.W. 10	
1896		Thomson, George Ritchie, C.M.G., M.B., C.M., formerly Professor of Surgery, University of the Witwatersrand, Johannesburg, Transvaal. Hordle Grange, Hordle, Hants	
1903		Thomson, George S., Kenmore Farm, Whelpley Hill, Chesham, Bucks	
1906		Thomson, Gilbert, M.A., M.Inst.C.E., 164 Bath Street, Glasgow, C. 2	
1926		* Thomson, Godfrey Hilton, D.Sc., Ph.D., Professor of Education, University of Edinburgh (Moray House)	1931–34.

Date of Election			Service on Council, etc.
1926	C.	* Thomson, John, M.A., Ph.D. (Glas.), Lecturer in Plant Physiology, University of Glasgow. 2 Chartwell Terrace, Bearsden, Glasgow	
1934		* Thomson, Matthew Sydney, M.A., M.D., B.Ch. (Cantab.), F.R.C.P., M.R.C.S., Physician for Diseases of the Skin, King's College Hospital, Belgrave Hospital for Children. 106 Harley Street, London, W. 1	
1912		Thomson, R. Tatlock, F.I.C., 156 Bath Street, Glasgow	
1938		* Thomson, Robert, B.Sc., Mech.Eng., A.M.I.Mech.E., Ph.D. (Edin.), Education Officer, Air Ministry. Moorfield, Terrick Road, Butler's Cross, Aylesbury, Bucks	
1882		Thomson, Sir William, Kt., M.A., B.Sc., LL.D., formerly Principal, University of the Witwatersrand. Dunedin, Glencairn, Simonstown, South Africa	
1917		* Thorneycroft, Wallace, J.P., Chalmington, Dorchester	
1933		* Timms, Geoffrey, Ph.D. (Cantab.), Lecturer in Mathematics, University of St Andrews. Deanscourt, St Andrews	
1937		* Tod, Henry, B.Sc., Ph.D. (Edin.), Biochemist, The Royal Edinburgh Hospital. 35 Oxgangs Road, Edinburgh 10	
1920		* Todd, John Barber, B.Sc., Ph.D., M.I.Mech.E., Reader in Engineering, University of Edinburgh. 4 Bright's Crescent, Edinburgh 9	
1938		* Topping, Andrew, T.D., M.A. M.D., D.P.H. (Aberd.), A Senior Medical Officer, Public Health Department, London County Council. 29 Lee Terrace, Blackheath, London, S.E. 6	
1917		* Tovey, Sir Donald Francis, Kt., B.A. (Oxon.), M.Mus. (Hon.), Birmingham, Professor of Music, University of Edinburgh (Reid School of Music). 39 Royal Terrace, Edinburgh 7	
1914		† Tredgold, Alfred Frank, M.D. (Durham), F.R.C.P. (Lond.), Lecturer on Mental Deficiency, University of London. St Martins, Guildford	
1915		* Trotter, George Clark, M.D. (Edin.), D.P.H. (Aberd.), F.S.A.Scot., Medical Officer of Health, Metropolitan Borough, Islington. Braemar, 17 Haslemere Road, Crouch End, London, N. 8	
1938		* Trueman, Arthur Elijah, D.Sc., F.G.S., Professor of Geology, University of Glasgow. 20 Queensborough Gardens, Glasgow	
1922	C. K.	* Turnbull, Herbert Westren, M.A., F.R.S., Professor of Mathematics, University of St Andrews. Randa, Hepburn Gardens, St Andrews	1928–31.
1937		* Turnbull, Mathew McKerrow, M.A. (Edin.), Lecturer in Banking, University of Edinburgh (South Bridge). 14 Minto Street, Edinburgh 9	
1905		† Turner, Arthur Logan, M.D., LL.D., F.R.C.S.E., 27 Walker Street, Edinburgh 3	1926–29. V-P 1930–33.
1925		* Turner, Harry Moreton Stanley, M.B.E., M.D., M.R.C.S., L.R.C.P., D.T.M. and H., Chevalier de l'Ordre Royale du Sauveur de Grèce. Wing Commander, R.A.F. (retired). The Haven, Brookwood, Surrey	
1924		* Turner, Richard, O.B.E., M.B., C.M., Hotel Hydropathic, Peebles	
1918	C. N.	* Tyrrell, George Walter, A.R.C.S., D.Sc., F.G.S., Lecturer in Petrology, Geological Department, University of Glasgow	1926–29. 1937–
1930	C.	* Voge, Cecil Innes Bothwell, Ph.D. (Edin.), 46 Roxborough Park, Harrow-on-the-Hill, London	
1932		* Wade, Henry, C.M.G., D.S.O., M.D., Senior Lecturer in Clinical Surgery, University of Edinburgh (Royal Infirmary). 6 Manor Place, Edinburgh 3	
1926		* Wakeley, Cecil Pembrey Grey, F.R.C.S., Surgeon to King's College Hospital, London, Lecturer in Anatomy, King's College, London. 14 Devonshire Street, Portland Place, London, W. 1	
1925	C.	* Walker, Frederick, M.A., Ph.D., D.Sc., Professor of Mineralogy and Geology, The University, Cape Town	
1938		* Walker, Oswald James, B.Sc., Ph.D. (Edin.), Lecturer in Chemistry, University College, Gower Street, London, W.C. 1	
1931		* Walker, William James Stirling, Ph.D. (Edin.), A.H.-W.C., F.I.C., F.I.L., F.S.A. Scot., Scientific Officer, H.M. Fuel Research Station, East Greenwich, London, S.E. 10. 13, The Lawns, Lee Terrace, Blackheath, London, S.E. 3	
1902		Wallace, Alexander G., M.A., 56 Fonthill Road, Aberdeen	
1886	C.	Wallace, Robert, M.A., LL.D., F.L.S., Emeritus Professor of Agriculture and Rural Economy, University of Edinburgh. Mid Park House, Kincardine-on-Forth, Fife	
1898		Wallace, William, M.A., Campsie, Alta, Canada	

Date of Election			Service on Council, etc.
1920		* Walmsley, Thomas, M.D. (Glas.), Professor of Anatomy, Queen's University, Belfast	
1931	C.	* Walton, John, M.A. (Cantab.), D.Sc. (Manchester) (VICE-PRESIDENT), Regius Professor of Botany, University of Glasgow. 23 Lilybank Gardens, Glasgow, W. 2	1934–37. V-P 1937–
1927	C.	* Wardlaw, Claude Wilson, D.Sc. (Glas.), Imperial College of Tropical Agriculture, Trinidad, B.W.I.	
1936		* Warr, The Very Rev. Charles Laing, C.V.O., M.A., D.D., LL.D., Hon. R.S.A., Dean of the Thistle and of the Chapel Royal in Scotland, Chaplain to H.M. The King, Minister of St Giles' Cathedral, Edinburgh. 63 Northumberland Street, Edinburgh 3	
1923		* Warren, John Alexander, M.Inst.C.E. 74 Balshagray Avenue, Partick, Glasgow	
1901	C.	Waterston, David, M.A., M.D., F.R.C.S.E., Professor of Anatomy, University of St Andrews	1916–19, 1925–28
1927		* Watson, Charles Brodie Boog, F.S.A.Scot. 24 Garscube Terrace, Edinburgh 12	
1923		* Watson, H. Ferguson, M.D., F.R.F.P.S., Ph.D., D.P.H. (Glas.), formerly H.M. Senior Deputy Commissioner, General Board of Control for Scotland. 109 Montgomery Street, Edinburgh 7	
1923	C.	* Watson, William, M.A., B.Sc. (Edin.), Lecturer in Physics, Heriot-Watt College, Edinburgh. 17 Braidburn Crescent, Edinburgh 10	
1911		† Watt, James, W.S., F.F.A., LL.D. (VICE-PRESIDENT), 7 Blackford Road, Edinburgh 9	1924–26. Treasurer 1926–37. V-P 1937–
1933		* Watt, John Mitchell, M.B., Ch.B., M.R.C.P. (Edin.), F.R.S.S.A., Professor of Pharmacology, University of the Witwatersrand, Johannesburg, South Africa	
1911		Watt, Very Rev. Lauchlan MacLean, M.A., D.D., LL.D., Kinloch, Lochcarron, Ross-shire	
1928		* Watters, Alexander Marshall, M.A., B.Sc. (Glas.), Rector of Hawick High School. High School House, Hawick	
1896		† Webster, John Clarence, C.M.G., M.D., D.Sc., LL.D., F.R.C.P.E., formerly Professor of Obstetrics and Gynæcology, Rush Medical College, Shediac, N.B., Canada	
1907	C. M-B.	† Wedderburn, Ernest Maclagan, O.B.E., M.A., D.Sc., LL.D., Deputy Keeper of the Signet (TREASURER). 6 Succoth Gardens, Edinburgh 12	1913–16, 1921–24, 1932–35, 1936–37. Treasurer 1937–
1903	C. M-B.	† Wedderburn, J. H. Maclagan, M.A., D.Sc., F.R.S., Professor of Mathematics, Princeton University. Fine Hall, Princeton, N.J., U.S.A.	
1904		Wedderspoon, William Gibson, M.A., LL.D.	
1934	C.	* Weir, John, M.A., Ph.D., D.Sc. (Glas.), Lecturer in Palæontology, University of Glasgow. 18 Botanic Crescent, Glasgow, N.W.	
1930		* White, Adam Cairns, M.B., Ch.B., Ph.D., Assistant Pharmacologist, Wellcome Physiological Research Laboratory, Beckenham, Kent	
1933		* Whitley, William Frederic James, M.D. (Edin.), D.P.H. (Oxon.), Medical Officer of Health, Northumberland County Council. Westfield, Cramlington, Northumberland	
1931		* Whitson, Sir Thomas Barnby, D.L., LL.D., C.A., Lord Provost of the City of Edinburgh (1929–32). 27 Eglinton Crescent, Edinburgh 12	
1911		Whittaker, Charles Richard, F.R.C.S.E., F.S.A.Scot., Lynwood, Hatton Place, Edinburgh 9	
1912	C. V. J. B-P.	Whittaker, Edmund Taylor, M.A., Hon. Sc.D. (Dubl.), Hon. LL.D. (St Andrews and California), F.R.S., Foreign Member of the R. Accademia dei Lincei, Rome, Member of the Pontifical Academy of Sciences (VICE-PRESIDENT), Professor of Mathematics, University of Edinburgh (16 Chambers Street). 48 George Square, Edinburgh 8	1912–15, 1922–25. Sec. 1916–22. V-P 1925–28, 1937–
1928	C.	* Whittaker, John Macnaghten, M.A. (Edin.), M.A. (Cantab.), D.Sc., Professor of Pure Mathematics, University of Liverpool	

Date of Election			Service on Council, etc.
1936		* Whyte, Andrew, A.C.A., F.R.G.S., Chartered Accountant. The Knoll, 1 Linden Avenue, Darlington	
1918		* Whyte, Rev. Charles, M.A., LL.D., F.R.A.S., U.F. Church Manse, Kingswells, Aberdeen	
1935		* Whyte, Sir William Edward, Kt., O.B.E., J.P., Solicitor. Balgay, Uddingston	
1934		* Whyte, William, Cashier and General Manager of the Royal Bank of Scotland. Baberton House, Juniper Green, Edinburgh	
1929	C.	* Wiesner, Bertold Paul, D.Sc., formerly Macaulay Lecturer, Institute of Animal Genetics, University of Edinburgh. 37 Great Cumberland Place, London, W. 1	
1918		* Wight, John Thomas, M.I.Mech.E., M.I.Mar.E., Joint Managing Director, Messrs MacTaggart, Scott & Co., Ltd., Loanhead. Calderwood Villa, Lasswade	
1934		* Wightman, William Persehouse Delisle, Ph.D., M.Sc. (Lond.), Science Master, Edinburgh Academy. 36 Coltbridge Terrace, Edinburgh 12	
1926	C. N.	* Williams, Samuel, Ph.D., Lecturer in Plant Morphology, University of Glasgow. 27 Lindsay Place, Kelvindale, Glasgow	
1908		Williamson, Henry Charles, M.A., D.Sc., formerly Naturalist to the Fishery Board for Scotland. 13 Windsor Street, Dundee	
1928	C.	* Williamson, John, M.A. (Edin.), Ph.D. (Chicago), Associate Professor of Mathematics, Johns Hopkins University, Baltimore, U.S.A.	
1910	C.	Williamson, William, F.L.S., 47 St Alban's Road, Edinburgh 9	
1927	C.	* Williamson, William Turner Horace, B.Sc. (Aberd.), Ph.D. (Edin.), Chief Chemist, Egyptian Ministry of Agriculture, Cotton Research Board, Giza, Egypt	
1911		Wilson, Andrew, O.B.E., D.L., M.Inst.C.E. 51 Queen Street, Edinburgh 2	
1902	V. J.	† Wilson, Charles Thomson Rees, C.H., M.A., LL.D., D.Sc., F.R.S., Nobel Prize, Physics, 1927, Emeritus Professor of Natural Philosophy, University of Cambridge. 196 Grange Loan, Edinburgh 9	1937–
1922		* Wilson, John, F.R.I.B.A., Chief Architect, Scottish Department of Health. 20 Lomond Road, Edinburgh 5	
1920	C.	* Wilson, Malcolm, D.Sc. (London), A.R.C.S., F.L.S., Reader in Mycology and Bacteriology, University of Edinburgh (Royal Botanic Garden). Brent Knoll, Kinnear Road, Edinburgh 4	1931–34.
1938		* Wilson, Robert, Master Printer, Partner of Messrs H. and J. Pillans & Wilson, Edinburgh. 13 Corrennie Drive Edinburgh, 10	
1924		* Wilson, William, M.A., LL.B., Advocate, Regius Professor of Public Law, University of Edinburgh (South Bridge). 38 Moray Place, Edinburgh 3	
1895		Wilson-Barker, Sir David, Kt., R.D., R.N.R., F.R.G.S., formerly Captain-Superintendent, Thames Nautical Training College, H.M.S. "Worcester." 12 Bolan Street, London, S.W. 11	
1934		* Winstanley, Arthur, M.B.E., D.Sc. (Eng.) (Lond.), M.I.Min.E., Mining Engineer to Safety in Mines Research Board. 18 St John's Road, Edinburgh 12	
1931	C.	* Wishart, John, M.A., B.Sc. (Edin.), M.A. (Cantab.), D.Sc. (Lond.), Reader in Statistics, University of Cambridge. Croft Lodge, Barton Road, Cambridge	
1922	C. B.	* Wordie, James Mann, M.A. (Cantab.), B.Sc. (Glas.), St John's College, Cambridge	
1937		* Wright, Edward Maitland, B.A. (Lond.), M.A., D.Phil. (Oxon.), Professor of Mathematics, University of Aberdeen. 52 College Bounds, Aberdeen.	
1933		* Wright, James, F.G.S.. Balado, 212 Colinton Road, Edinburgh 11	
1896		† Wright, Sir Robert Patrick, LL.D., formerly Chairman of the Board of Agriculture for Scotland. The Heugh, North Berwick, East Lothian	
1911	C.	Wrigley, Ruric Whitehead, M.A. (Cantab.), Assistant Astronomer, Royal Observatory, Edinburgh	
1938		* Wyburn, George McCreath, M.B., Ch.B. (Glas.), F.R.F.S.P.G., Lecturer in Anatomy, University of Glasgow	
1937	C.	* Young, Andrew White, M.A., B.Sc., LL.B. (Edin.), W.S. 15 Great Stuart Street, Edinburgh 3	
1882		Young, Frank W., C.B.E., F.C.S., H.M. Inspector of Schools (Emeritus). Panera, Shortheath, Farnham, Surrey	
1904		Young, Robert B., M.A., D.Sc., F.G.S., Professor of Geology, University of the Witwatersrand (South African School of Mines and Technology), Johannesburg, Transvaal	

Number of Fellows, 753.

HONORARY FELLOWS OF THE SOCIETY.

(*At 24th October* 1938.)

1920 HIS ROYAL HIGHNESS THE DUKE OF WINDSOR, K.G.

FOREIGNERS (LIMITED TO FORTY-FOUR BY LAW I).

Elected

1936 Leo Hendrik Baekeland, Professor (Honorary) of Chemical Engineering, Columbia University, New York. Bakelite Corporation, 247 Park Avenue, New York City.

1916 Charles Eugène Barrois, formerly Professor of Geology and Mineralogy, Université, Lille, France. 41, Rue Pascal, Lille.

1923 Henri Bergson, Honorary Professor, College of France, Paris.

1930 Vilhelm Frimann Koren Bjerknes, Professor of Physics, University of Oslo.

1937 Marston Taylor Bogert, Professor of Organic Chemistry, Columbia University, N.Y.

1927 Niels Bohr, Nobel Laureate, Physics, 1922, Professor of Physics, University of Copenhagen.

1927 Jules Bordet, Nobel Laureate, Medicine, 1919, Professor of Bacteriology, University of Brussels.

1933 Filippo Bottazzi, Professor of Experimental Physiology, Royal Institute of Physiology, S. Andrea delle Dame, 21, Naples.

1923 Marcellin Boule, Director of the Institute of Human Palæontology, 1, Rue René-Panhard, Paris, XIII^{e}.

1905 Waldemar Christofer Brögger, Professor of Mineralogy and Geology, K. Frederiks Universitet, Oslo.

1916 Douglas Houghton Campbell, Emeritus Professor of Botany, Stanford University, California.

1930 Walter Bradford Cannon, Professor of Physiology, Harvard University, Cambridge, Mass.

1930 Maurice Caullery, Professor of Zoology in the University of Paris. Laboratoire d'Évolution des Êtres organisés, 105 Bould. Raspail, Paris, VI^{e}.

1933 Edwin Grant Conklin, formerly Professor of Biology, Princeton University, N.J.

1921 Reginald Aldworth Daly, Professor of Geology, Harvard University, Cambridge, Mass.

1927 Albert Einstein, Nobel Laureate, Physics, 1921, Princeton University, N.J.

1938 Federigo Enriques, Professor of Mathematics, Royal University, Rome.

1934 Björn Helland-Hansen, Geophysical Institute, Bergen.

1921 Johan Hjort, Professor of Marine Biology, University, Oslo.

1923 Arnold Frederik Holleman, Emeritus Professor of Organic Chemistry, University, Amsterdam. Boekensteijn Parkweg 7, Bloemendaal.

1934 Bernardo Houssay, Professor of Physiology, National University of Buenos Aires.

1937 C. U. Ariëns Kappers, Director of the Central Institute of Brain Research, Amsterdam, and Professor of Comparative Neurology, University, Amsterdam.

1933 Nikolaj Konstantinovic Koltzoff, formerly Professor of Zoology, State University, Moscow; Director of the Research Institute of Experimental Biology. Moscow 64, Voronzovo Pole 6.

1923 Tullio Levi-Civita, Professor of Mathematics, Regia Università, Rome.

1934 Frank Rattray Lillie, Emeritus Professor of Zoology and Embryology, University of Chicago, and President, National Academy of Sciences, Washington, D.C.

1936 Maurice Lugeon, Professor of Geology, University, Lausanne.

1927 Hans Horst Meyer, Emeritus Professor of Pharmacology, University of Vienna.

1934 Thomas Hunt Morgan, Nobel Laureate, Medicine, 1933, Professor of Biology, California Institute of Technology, Pasadena.

1933 Albrecht Penck, Geheimrat, Emeritus Professor of Geography, Friedrich-Wilhelms-Universität, Berlin. Geographisches Institut, Universitäts-strasse 3*b*, Berlin, N.W. 7

1920 Charles Émile Picard, Perpetual Secretary, Academy of Sciences, Paris.

1937 Max Planck, Nobel Laureate, Physics, 1918, Professor Ordinarius Emeritus of Theoretical Physics, Director of the Institute for Theoretical Physics, University of Berlin.

1938 Henry Norris Russell, For.Mem.R.S., Chairman of the Department of Astronomy and Director of the Observatory, Princeton University, U.S.A.

1934 Paul Sabatier, Nobel Laureate, Chemistry, 1912, Professor of Chemistry, University of Toulouse.

1936 George Sarton, Editor of *Isis* and *Osiris*, Harvard Library, 185, Cambridge, Mass.

1930 Erik Helge Oswald Stensiö, Professor of Palæontology and Historical Geology, Royal University of Upsala.

1936 George Linius Streeter, Director, Department of Embryology, Carnegie Institution of Washington, Corner Wolfe and Madison Streets, Baltimore. 3707 St Paul Street, Baltimore, Md.

Elected

1938 Karl Freiherr von Tubeuf, Professor of Botany, University of Munich.

1936 Nikolai Ivanovic Vavilov, Director of the Institute of Plant Industry, Academy of Sciences, Leningrad, U.S.S.R.

1913 Vito Volterra, formerly Professor of Mathematical Physics, Regia Università. Villa Volterra, Ariccia, near Rome.

1927 Richard Willstätter, Nobel Laureate, Chemistry, 1915, formerly Professor of Chemistry, University of Munich.

1923 Edmund Beecher Wilson, formerly Professor of Zoology, Columbia University, New York.

1933 Pieter Zeeman, Nobel Laureate, Physics, 1902, Emeritus Professor of Physics, University, Amsterdam. Stadhouderskade 158, Amsterdam.

Total, 42.

BRITISH SUBJECTS (LIMITED TO TWENTY-TWO BY LAW I).

1937 John Logie Baird, Inventor of the Televisor. 3 Crescent Wood Road, Sydenham, London, S.E.

1936 Sir Charles Vernon Boys, Kt., A.R.S.M., LL.D., F.R.S., St Marybourne, Andover.

1927 Sir William Henry Bragg, O.M., K.B.E., M.A., D.Sc., LL.D., President R.S., Nobel Laureate, Physics, 1915, Fullerian Professor of Chemistry, Royal Institution, London.

1937 William Thomas Calman, C.B., D.Sc., LL.D (St Andrews), F.R.S., formerly Keeper of Zoology, British Museum. 24 Lexham Gardens, London, W. 8.

1936 Sir Henry Hallett Dale, Kt., C.B.E., M.D., Hon. D.Sc., F.R.S., Joint Nobel Laureate, Medicine, 1936, Director of the National Institute for Medical Research, Mount Vernon, London, N.W. 3.

1936 Frederick George Donnan, C.B.E., M.A., Ph.D., D.Sc., LL.D., F.R.S., formerly Professor of Chemistry, University of London, and Director of Chemical Laboratories, University College. 23 Woburn Square, London, W.C. 1

1930 Sir Arthur Stanley Eddington, O.M., Kt., M.A., Hon. D.Sc., LL.D., F.R.S., Plumian Professor of Astronomy and Experimental Philosophy, University of Cambridge.

1927 Sir John Bretland Farmer, Kt., M.A., D.Sc., LL.D., F.R.S., Emeritus Professor of Botany, Imperial College of Science and Technology, London. St Leonard's, Weston Road, Bath.

1900 Andrew Russell Forsyth, M.A., Sc.D., LL.D.. Hon. Math.D., F.R.S., Emeritus Professor of Mathematics, Imperial College of Science and Technology, London; formerly Sadleirian Professor of Pure Mathematics, University of Cambridge.

1910 Sir James George Frazer, Kt., O.M., D.C.L., LL.D., Litt.D., F.B.A., F.R.S., Commandeur de la Légion d'Honneur. Trinity College, Cambridge.

1927 Sir Frederick Gowland Hopkins, O.M., Kt., M.A., M.B., Hon. D.Sc., LL.D., Past President R.S., Joint Nobel Laureate, Medicine, 1929, Sir William Dunn Professor of Biochemistry, University of Cambridge

1930 Sir Arthur Keith, Kt., M.D., LL.D., F.R.S., Master, Buckston Browne Research Farm, Downe, Farnborough, Kent.

1910 Sir Joseph Larmor, Kt., M.A., D.Sc., LL.D., D.C.L., F.R.S., formerly Lucasian Professor of Mathematics, University of Cambridge. St John's College, Cambridge.

1938 Sir Thomas Lewis, Kt., C.B.E., D.Sc., M.D., LL.D., F.R.S., Consulting Physician, Ministry of Pensions, Physician-in-Charge of Department of Clinical Research, University College Hospital, London.

1933 Sir George Macdonald, K.C.B., D.Litt., Litt.D., LL.D., F.B.A., formerly Secretary, Scottish Education Department. 17 Learmonth Gardens, Edinburgh 4.

1934 Sir Edward Bagnall Poulton, Kt., M.A., D.Sc., LL.D., F.R.S., formerly Hope Professor of Zoology, University of Oxford. Wykeham House, Banbury Road, Oxford.

1930 Robert Robinson, M.A., D.Sc., LL.D., F.R.S., Waynflete Professor of Chemistry, University of Oxford.

1933 Sir William Napier Shaw, Kt., Sc.D.(Cantab.), LL.D., F.R.S., formerly Director Meteorological Office. 10 Moreton Gardens, London, S.W. 5.

1908 Sir Charles Scott Sherrington, O.M., G.B.E., M.A., D.Sc., M.D., LL.D., Past President R.S., Joint Laureate, Nobel Prize, Medicine, 1932, formerly Waynflete Professor of Physiology, University of Oxford. Broomside, Valley Road, Ipswich.

1938 Geoffrey Ingram Taylor, M.A., Hon.D.Sc., F.R.S., Yarrow Research Professor of the Royal Society, Fellow of Trinity College, Cambridge.

1905 Sir Joseph John Thomson, O.M., Kt., D.Sc., LL.D., Past President R.S., Nobel Laureate Physics, 1906, formerly Cavendish Professor of Experimental Physics, now Professor of Physics, University of Cambridge, Master of Trinity College, Cambridge.

1934 William Whitehead Watts, Sc.D., M.Sc., LL.D., F.R.S., Emeritus Professor of Geology, Imperial College of Science and Technology, London. Hillside, Langley Park, Sutton, Surrey.

Total, 22.

CHANGES IN FELLOWSHIP DURING SESSION 1937–1938.

FELLOWS OF THE SOCIETY ELECTED.

CHARLES HENRY WILLIAM GATACRE ANDERSON.
PAUL BACSICH
DAVID ARMITAGE BANNERMAN
ALEXANDER WILLIAM MORTON BEVERIDGE.
GEOFFREY BERNARD BROOK.
CHARLES AUGUSTUS CARLOW.
SIR IAIN COLQUHOUN.
MARTIN MELVIN CRUICKSHANK.
STANLEY CURSITER.
JOHN MICHAEL DEWAR.
NORMAN McOMISH DOTT.
THE RIGHT HON. LORD ELPHINSTONE.
CHARLES HENRY PEARSON GIFFORD.
CECIL GORDON.
WILLIAM SMITH GORDON.
RAM KUMAR GOYAL.
JAMES ROBERTSON CAMPBELL GREENLEES.
GEORGE HOGARTH.
JAMES DALGLEISH HAMILTON JAMIESON.
ALLISTER MIDDLETON MACGILLIVRAY.
ALEXANDER MACKIE.
WILLIAM HUTCHISON McMILLAN.
DONALD MAINLAND.
CHARLES ALEXANDER MALCOLM.
SIR JOHN MAXWELL STIRLING MAXWELL.
HARRY HENDERSON MONTEATH.
SANFORD STERLING MUNRO.
THOMAS CRAWFORD PHEMISTER
ANDREW MAITLAND RAMSAY.
THE RT. HON. THE EARL OF ROSEBERY.
JAMES SANDILANDS.
ARTHUR HENRY HAVENS SINCLAIR.
JAMES STEWART.
JOHN LIVINGSTONE STEWART.
ARTHUR LANDSBOROUGH THOMSON.
ROBERT THOMSON.
ANDREW TOPPING.
ARTHUR ELIJAH TRUEMAN.
OSWALD JAMES WALKER.
ROBERT WILSON.
GEORGE McCREATH WYBURN.

HONORARY FELLOWS ELECTED.

FOREIGN.

FEDERIGO ENRIQUES, Rome.
HENRY NORRIS RUSSELL, Princeton.
KARL FREIHERR VON TUBEUF, Munich.

BRITISH.

SIR THOMAS LEWIS, London.
GEOFFREY INGRAM TAYLOR, Cambridge.

FELLOWS DECEASED.

O. CHARNOCK BRADLEY.
SIR CHARLES BRIGHT.
REV. THOMAS BURNS.
SIR JOHN JAMES BURNET.
WILLIAM EAGLE CLARKE.
SIR JAMES CRICHTON-BROWNE.
ALEXANDER JOHN DEY.
MALCOLM JAMES ROWLEY DUNSTAN.
ALEXANDER GALT.
SIR WILLIAM CAMPBELL JOHNSTON.
SIR WILLIAM COLIN MACKENZIE.
EDALJI MANEKJI MODI (*Died*, 13*th September* 1924).
SIR ROBERT LUDWIG MOND.
WILLIAM CARSTAIRS REID.
HON. ALEXANDER WILLIAM ROBERTS.
DAVID ALAN STEVENSON.
ROBERT BLACK THOMSON.
JOHN EDWARD TOUCHE.
SIR DAVID PERCIVAL DALBRECK WILKIE.

FOREIGN HONORARY FELLOWS DECEASED.

JOHN JACOB ABEL.
WILLIAM WALLACE CAMPBELL.
GEORGE ELLERY HALE.

FELLOWS RESIGNED.

THOMAS ALTY.
ROBERT GORDON CARRUTHERS.
GEORGE SAMUEL EASTWOOD.
JOHN MILLER WOODBURN MORISON.

FELLOWS REMOVED FROM ROLL.

GEORGE TOPHAM FORREST.
L. W. GORDON MALCOLM.
ALEXANDER STEVENS.

LAWS OF THE SOCIETY.

Adopted July 3, 1916; *amended December* 18, 1916.

LAW I, amended February 5, 1934.
„ VI, „ „ 7, 1921.
„ „ „ July 2, 1928.
„ VIII, „ May 3, 1920.
LAW IX, amended May 3, 1920.
„ XIII, „ May 3, 1920.
„ XIX, „ June 16, 1924.

I.

THE ROYAL SOCIETY OF EDINBURGH, which was instituted by Royal Charter in 1783 for the promotion of Science and Literature, shall consist of Ordinary Fellows (hereinafter to be termed Fellows) and Honorary Fellows. The number of Honorary Fellows shall not exceed sixty-six, of whom not more than twenty-two may be British subjects, and not more than forty-four subjects of Foreign States.

Fellows only shall be eligible to hold office or to vote at any Meeting of the Society.

ELECTION OF FELLOWS.

II.

Each Candidate for admission as a Fellow shall be proposed by at least four Fellows, two of whom must certify from personal knowledge. The Official Certificate shall specify the name, rank, profession, place of residence, and the qualifications of the Candidate. The Certificate shall be delivered to the General Secretary before the 30th of November, and, subject to the approval of the Council, shall be exhibited in the Society's House during the month of January following. All Certificates so exhibited shall be considered by the Council at its first meeting in February, and a list of the Candidates approved by the Council for election shall be issued to the Fellows not later than the 21st of February.

III.

The election of Fellows shall be by Ballot, and shall take place at the first Ordinary Meeting in March. Only Candidates approved by the Council shall be eligible for election. A Candidate shall be held not elected, unless he is supported by a majority of two-thirds of the Fellows present and voting.

IV.

On the day of election of Fellows two scrutineers, nominated by the President, shall examine the votes and hand their report to the President, who shall declare the result.

V.

Each Fellow, after his election, is expected to attend an Ordinary Meeting, and sign the Roll of Fellows, he having first made the payments required by Law VI. He shall be introduced to the President, who shall address him in these words:—

> *In the name and by the authority of THE ROYAL SOCIETY OF EDINBURGH, I admit you a Fellow thereof.*

PAYMENTS BY FELLOWS.

VI.

Each Fellow shall, before he is admitted to the privileges of Fellowship, pay an admission fee of three guineas, and a subscription of three guineas for the year of election. He shall continue to pay a subscription of three guineas at the beginning of each session so long as he remains a Fellow.

Each Fellow who was elected subsequent to December 1916 and previous to December 1920 shall also pay a subscription of three guineas at the beginning of each session so long as he remains a Fellow.

Each Fellow who was elected previous to December 1916, and who has not completed his twenty-five annual payments, shall, at the beginning of each session, pay three guineas until his twenty-five annual payments are made. Each Fellow who has completed or shall complete his payments shall be invited to contribute one guinea per annum or to pay a single sum of ten guineas.

A Fellow may compound for the annual subscriptions by a single payment of fifty guineas, or on such other terms as the Council may from time to time fix.

VII.

A Fellow who, after application made by the Treasurer, fails to pay any contribution due by him, shall be reported to the Council, and, if the Council see fit, shall be declared no longer a Fellow. Notwithstanding such declaration all arrears of contributions shall remain exigible.

ELECTION OF HONORARY FELLOWS.

VIII.

Honorary Fellows shall be persons eminently distinguished in Science or Literature. They shall not be liable to contribute to the Society's Funds. Personages of the Blood Royal may be elected Honorary Fellows at any time on the nomination of the Council, and without regard to the limitation of numbers specified in Law I.

IX.

Honorary Fellows shall be proposed by the Council. The nominations shall be announced from the Chair at the First Ordinary Meeting after their selection. The names shall be printed in the circular for the last Ordinary Meeting of the Session, when the election shall be by Ballot, after the manner prescribed in Laws III and IV for the Election of Fellows.

EXPULSION OF FELLOWS.

X.

If, in the opinion of the Council, the conduct of any Fellow is injurious to the character or interests of the Society, the Council may, by registered letter, request him to resign. If he fail to do so within one month of such request, the Council shall call a Special Meeting of the Society to consider the matter. If a majority consisting of not less than two-thirds of the Fellows present and voting decide for expulsion, he shall be expelled by declaration from the Chair, his name shall be erased from the Roll, and he shall forfeit all right or claim in or to the property of the Society.

XI.

It shall be competent for the Council to remove any person from the Roll of Honorary Fellows if, in their opinion, his remaining on the Roll would be injurious to the character or interests of the Society. Reasonable notice of such proposal shall be given to each member of the Council, and, if possible, to the Honorary Fellow himself. Thereafter the decision on the question shall not be taken until the matter has been discussed at two Meetings of Council, separated by an interval of not less than fourteen days. A majority of two-thirds of the members present and voting shall be required for such removal.

MEETINGS OF THE SOCIETY.

XII

A Statutory Meeting for the election of Council and Office-Bearers, for the presentation of the Annual Reports, and for such other business as may be arranged by the Council, shall be held on the fourth Monday of October. Each Session of the Society shall begin at the date of the Statutory Meeting.

XIII.

Meetings for reading and discussing communications and for general business, herein termed Ordinary Meetings, shall be held, when convenient, on the first and third Mondays of each month from November to July inclusive, with the exception that in January the meetings shall be held on the second and fourth Mondays.

XIV.

A Special Meeting of the Society may be called at any time by direction of the Council, or on a requisition to the Council signed by not fewer than six Fellows. The date and hour of such Meeting shall be determined by the Council, who shall give not less than seven days' notice of such Meeting. The notice shall state the purpose for which the Special Meeting is summoned; no other business shall be transacted.

PUBLICATION OF PAPERS.

XV.

The Society shall publish Transactions and Proceedings. The consideration of the acceptance, reading, and publication of papers is vested in the Council, whose decision shall be final. Acceptance for reading shall not necessarily imply acceptance for publication.

DISTRIBUTION OF PUBLICATIONS.

XVI.

Fellows who are not in arrear with their Annual Subscriptions and all Honorary Fellows shall be entitled gratis to copies of the Parts of the Transactions and the Proceedings published subsequently to their admission.

Copies of the Parts of the Proceedings shall be distributed by post or otherwise, as soon as may be convenient after publication; copies of the Transactions or Parts thereof shall be obtainable upon application, either personally or by an authorised agent, to the Librarian, provided the application is made within five years after the date of publication.

CONSTITUTION OF COUNCIL.

XVII.

The Council shall consist of a President, six Vice-Presidents, a Treasurer, a General Secretary, two Secretaries to the Ordinary Meetings (the one representing the Biological group and the other the Physical group of Sciences),* a Curator of the Library and Museum, and twelve ordinary members of Council.

ELECTION OF COUNCIL

XVIII.

The election of the Council and Office-Bearers for the ensuing Session shall be held at the Statutory Meeting on the fourth Monday of October. The list of the names recommended by the Council shall be issued to the Fellows not less than one week before the Meeting. The election shall be by Ballot, and shall be determined by a majority of the Fellows present and voting. Scrutineers shall be nominated as in Law IV.

XIX.

The President may hold office for a period not exceeding five consecutive years; the Vice-Presidents, not exceeding three; the Secretaries to the Ordinary Meetings, not exceeding five; the General Secretary, the Treasurer, and the Curator of the Library and Museum, not exceeding ten; and ordinary members of Council, not exceeding three consecutive years; provided that the Treasurer may be re-elected for more than ten successive years in cases where the Council declares to the Society that an emergency exists.

XX.

In the event of a vacancy arising in the Council or in any of the Offices enumerated in Law XVII, the Council shall proceed, as soon as convenient, to elect a Fellow to fill such vacancy for the period up to the next Statutory Meeting.

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* The Biological group includes Anatomy, Anthropology, Botany, Geology, Pathology, Physiology, Zoology; the Physical group includes Astronomy, Chemistry, Mathematics, Metallurgy, Meteorology, Physics.

POWERS OF THE COUNCIL.

XXI.

The Council shall have the following powers:—(1) To manage all business concerning the affairs of the Society. (2) To decide what papers shall be accepted for communication to the Society, and what papers shall be printed in whole or in part in the Transactions and Proceedings. (3) To appoint Committees. (4) To appoint employees and determine their remuneration. (5) To award the various prizes vested in the Society, in accordance with the terms of the respective deeds of gift, provided that no member of the existing Council shall be eligible for any such award. (6) To make from time to time Standing Orders for the regulation of the affairs of the Society. (7) To control the investment or expenditure of the Funds of the Society.

At Meetings of the Council the President or Chairman shall have a casting as well as a deliberative vote.

DUTIES OF PRESIDENT AND VICE-PRESIDENTS.

XXII.

The President shall take the Chair at Meetings of Council and of the Fellows. It shall be his duty to see that the business is conducted in accordance with the Charter and Laws of the Society. When unable to be present at any Meetings or attend to current business, he shall give notice to the General Secretary, in order that his place may be supplied. In the absence of the President his duties shall be discharged by one of the Vice-Presidents.

DUTIES OF THE TREASURER.

XXIII.

The Treasurer shall receive the monies due to the Society and shall make payments authorised by the Council. He shall lay before the Council a list of arrears in accordance with Rule VII. He shall keep accounts of all receipts and payments, and at the Statutory Meeting shall present the accounts for the preceding Session, balanced to the 30th of September, and audited by a professional accountant appointed annually by the Society.

DUTIES OF THE GENERAL SECRETARY.

XXIV.

The General Secretary shall be responsible to the Council for the conduct of the Society's correspondence, publications, and all other business except that which relates to finance. He shall keep Minutes of the Statutory and Special Meetings of the Society and Minutes of the Meetings of Council. He shall superintend, with the aid of the Assistant Secretary, the publication of the Transactions and Proceedings. He shall supervise the employees in the discharge of their duties.

DUTIES OF SECRETARIES TO ORDINARY MEETINGS.

XXV.

The Secretaries to Ordinary Meetings shall keep Minutes of the Ordinary Meetings. They shall assist the General Secretary, when necessary, in superintending the publication of the Transactions and Proceedings. In his absence, one of them shall perform his duties.

DUTIES OF CURATOR OF LIBRARY AND MUSEUM.

XXVI.

The Curator of the Library and Museum shall have charge of the Books, Manuscripts, Maps, and other articles belonging to the Society. He shall keep the Card Catalogue up to date. He shall purchase Books sanctioned by the Council.

ASSISTANT SECRETARY AND LIBRARIAN.

XXVII.

The Council shall appoint an Assistant Secretary and Librarian, who shall hold office during the pleasure of the Council. He shall give all his time, during prescribed hours, to the work of the Society, and shall be paid according to the determination of the Council. When necessary he shall act under the Treasurer in receiving subscriptions, giving out receipts, and paying employees.

ALTERATION OF LAWS.

XXVIII.

Any proposed alteration in the Laws shall be considered by the Council, due notice having been given to each member of Council. Such alteration, if approved by the Council, shall be proposed from the Chair at the next Ordinary Meeting of the Society, and, in accordance with the Charter, shall be considered and voted upon at a Meeting held at least one month after that at which the motion for alteration shall have been proposed.

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